Group density estimates for lar gibbons (*Hylobates lar)* and siamangs (*Symphalangus syndactylus)* and a quantitative analysis of the vegetative characteristics of the Sikundur Field Site.

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Southeast Asia's tropical forests encompass 20-25% of the world's plant and animal species. However, at the moment, this region is in the midst of a biodiversity crisis since it is experiencing a higher rate of forest loss than any other region. Indonesia has one of the highest deforestation rates globally, it experienced a total loss of 0.84 Mha of primary forest cover in 2012, with 51% of this loss occurring in lowland forests. Habitat loss and degradation challenge the survival and persistence of all forest vertebrates and create critical problems for arboreal animals, such as gibbons and siamangs. Gibbons and siamangs are arboreal primates, dependent on closed continuous canopies for feeding and travelling. Apart from information from the Sabangau Catchment in central Kalimantan, there is very limited data available for these primate populations across Indonesia. This study aims to identify which forest structure components are important indicators of habitat suitability for lar gibbons and siamangs. Lar gibbon and siamang group densities were determined at a field site in Sumatra, Indonesia, and it was investigated whether there was a difference across three disturbed land unit types (*Alluvial, Plains, Hills*) in gibbon and siamang densities and vegetation characteristics

Primate densities were calculated using auditory sampling methods at three sets of listening posts, while forest structure was analysed for 30 500m long line transects and 15 25 x 25m plots. Primate group densities were calculated using spatially explicit capture-recapture models. The results showed that the *Alluvial* land unit had the highest primate densities, as well as larger trees and greater availabilities of various branch sizes than the other land units. Furthermore, the *Plains* showed lower frequencies of tall trees >25m and had the lowest gibbon and siamang densities. These first analyses at this site support the prediction that the most suitable habitat for the highly arboreal gibbons and siamang contains mature large trees with a variation in branch supports.

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BA – Basal Area

DBH – Diameter at Breast Height

ESA – Effective Sampling Area

GLNP – Gunung Leuser National Park

IUCN – the International Union for Conservation of Nature

Mha – Million Hectares

NE – Northeast

NW – Northwest

PA – Protected Area

PAST – Paleontological Statistics

PCQM – Point-Centre-Quarter-Method

REDD – Reduced Emissions from Deforestation and Forest Degradation

SBA – Stand Basal Area

SE – Southeast

SECR – Spatially Explicit Capture Recapture

SOCP – Sumatran Orang-utan Conservation Program

SW– Southwest

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1. INTRODUCTION

1.1 Overview

Globally, tropical forests are some of the principal hotspots for the earth's biodiversity (Myers et al. 2000). Southeast Asia, as a region, is recognized for its contributions to biodiversity as it demonstrates to have very high species richness and endemism (Sodhi et al. 2010; Wilcove et al. 2013). However, at the moment, Southeast Asia is in the midst of a biodiversity crisis since this region is experiencing higher rates of forest loss than any other region (Sodhi et al. 2010). This study focuses on Indonesia, as this country experienced a total loss of 0.84 Mha of primary forest cover in 2012, where 51% of this forest loss occurred in lowland forests (Margono et al. 2014). In light of these results, the primate family, Hylobatidae, which includes lar gibbons (*Hylobates lar*) and siamangs (*Symphalangus syndactylus*) are of utmost concern since their distributions are largely restricted to Southeast Asia and these primates commonly inhabit lowland forests. The effects of deforestation can be detrimental to their survival since forest loss reduces the existence of continuous canopies that these primates are dependent upon (O'Brien and Kinnaird 2011). At the current moment, new field data is needed to fill in the gaps in knowledge regarding their population sizes and general living requirements, thus this study will collect original group density data for lar gibbons and siamangs across three land units in the Sikundur region of North Sumatra. Furthermore, this study will also quantify the forest structure to help identify key structural components of gibbon and siamang habitat sites.

1.2 Forest Ecosystems and Habitat Degradation

Southeast Asia's tropical forests encompass 20-25% of the world's plant and animal species (Woodruff 2010). This region could potentially lose up to three quarters of its original forests, as well as 42% of its biodiversity by 2100 if the rates of habitat loss of 1.4% per year are maintained (Sodhi et al. 2004). The primary drivers of land-use change within Southeast Asia can be grouped into three categories: 1) forest degradation by intensive logging; 2) conversion of forest areas into large-scale plantations; and 3) expansion of small-holder dominated farming areas (Miettinen et al. 2011). Forest dwelling vertebrates, such as primates, are likely to be negatively affected at population and community levels from anthropogenic land activities (Gouveia et al. 2014) because these disturbances modify vegetation structures and species compositions of residual stands. Accordingly, the scientific community requires current field studies to examine the dependence of arboreal primate

populations on the vertical organization of forests. This specific type of data will provide a more comprehensive understanding of the multi-dimensional relationships that exists between arboreal primates and their forest habitats. Furthermore, these studies will help identify the effects of habitat degradation on vertebrates that are highly dependent on forests.

Within Southeast Asia, Indonesia exhibits a long history of selective logging and consequently only 3.8% of Indonesia's forests are classified as primary (Cheyne et al. 2013). In addition, 61% of Indonesia's closed forests have been classified as production forests, specifically allocated to logging concessions (Cannon et al. 1994). In recent years, the conversion of forested land to agricultural plantations, such as palm oil, has become increasingly common, specifically in Sumatra. Primates such as gibbons and siamangs are continually threatened by these forest conversion practices due to the increasing amounts of forested land lost to monoculture plantations. For example, between the years 1995 and 2000, 40% of Sumatra's forests have been degraded and damaged by anthropogenic activities (O'Brien et al. 2004) and 15% of Sumatra's total land area has been allocated to plantation practices (YOSL-OIC 2009). Accordingly, anthropogenic land practices are expected to have the largest impact on biodiversity by 2100 through their influence on habitat availability and habitat quality (Sala et al. 2000).

1.3 Changes in Forest Structure and its Consequences

Anthropogenic land practices result in the modification of residual stand structures and vegetation characteristics of remaining forest habitats. For example, selective logging is responsible for altering the multi-layered forest canopy (Sodhi et al. 2004), by reducing canopy cover and creating canopy gaps (Hamard et al. 2010). In addition, forest encroachment disrupts the connectivity of forested areas and consequently creates discontinuous forest fragments of varying sizes (Yanuar and Chivers 2010). Forest fragmentation is a serious threat to biodiversity (Kakati et al. 2009) as it can inhibit gene flow and travel between habitat fragments and reduce species diversity. Similarly, palm oil plantations exhibit comparable effects on species diversity, habitat continuity and wildlife survival. Palm oil plantations support fewer species than natural forests and result in the marginalization of animal populations into degraded and fragmented habitats (YOSL-OIC 2009).

Habitat loss and degradation challenge the survival and persistence of all forest vertebrates; however, they specifically create critical problems for arboreal animals, including most Southeast Asian primates, such as gibbons and siamangs. Gibbons and siamangs are dependent on closed continuous canopies for feeding and travelling (O'Brien

and Kinnaird 2011) and frequently follow established routes known as "arboreal highways", which minimizes their chances of encountering gaps (Cheyne 2011). Unfortunately, discontinuous canopies and fragmented forests are becoming increasingly common as a result of human disturbance and consequently the energy costs of arboreal locomotion may increase dramatically as their direct routes of travel are impeded by canopy gaps (Cheyne 2011; Cheyne et al. 2013). The large gaps present between tree crowns and the uneven canopy continuity will require gibbons and siamangs to travel longer distances to reach their widely distributed and seasonal food sources (Cheyne 2011). Furthermore, uneven canopy continuity associated with human disturbances, such as logging, will lead to an increase in lower canopy vegetation growth. This will further incur additional travel costs since gibbons will be required to engage in various locomotor types, such as vertical climbing and leaping, more frequently as gaps are created from the removal of large trees (Vogel et al. 2009).

To date little information regarding habitat requirements for gibbons is available (Cheyne 2010). Future gibbon and siamang conservation is of utmost importance as all Indonesian gibbon and siamang species are presently listed as endangered on the IUCN Red List (Cheyne 2010) and population sizes continue to decline throughout Southeast Asia (O'Brien et al. 2011). Apart from the Sabangau Catchment in central Kalimantan, there is very limited data available for these primate populations across Indonesia (Cheyne 2010). This lack of data can be partially attributed to difficult detection and low visibility of the high canopy, as well as these primates' unreliable behaviour in response to human presence (Buckley et al. 2006). However, understanding the survival requirements of these arboreal primates is ever-more critical as their life history characteristics, such as long maturation periods, long inter-birth intervals and delayed age of first reproduction, reduces their potential to recover from low densities or population crashes (Buckley et al. 2006; Yanuar 2009; Phoonjampa et al. 2011; O'Brien and Kinnaird 2011). Specific forest characteristics, such as canopy stratification, are important in determining a primate's niche space within forests (Reed and Bidner 2004). Accordingly, it is imperative that habitat characteristics responsible for observed primate density differences are identified.

1.4 Research Aims, Objectives and Hypotheses

This study was conducted at Sikundur Monitoring Post, which is located in the Langkat district of North Sumatra, within Gunung Leuser National Park (GLNP). The focal species of this study were lar gibbons and siamangs. Lar gibbons and siamangs are small-sized apes classified under the superfamily *Homonoidea* (Bartlett 2007). These primates live an arboreal lifestyle and utilize the upper canopies for a large proportion of their daily activities

(Gittins and Raemaekers 1980). The Sikundur region primarily consists of lowland dipterocarp forest (Nowak 2013) and within this region three land units with different disturbance histories and varying topographies have been described (Laumonier 1997). These land units are identified as *Alluvial, Plains, and Hills*. Both the *Alluvial* and *Plains* land units feature flat terrain with undulating slopes and are typically found at low elevations, whereas the *Hills* land unit is situated at higher elevations (100-500 m) and has steeper terrain with elongated ridges at the top of its slopes. Accessibility differences amongst the land units have influenced the forest structure and vegetation found in each land unit, with the *Plains* and *Alluvial* land units having extensive disturbance histories with a more open forest structure as a result of their accessibility to villagers by roads and rivers (Laumonier 1997).

This study aims to identify which forest structure components are important indicators of habitat suitability for lar gibbons and siamangs. To do this, this study estimates lar gibbon and siamang group densities at a field site in Sumatra, Indonesia, and determines whether there is a difference across three disturbed land units in gibbon and siamang densities and vegetation characteristics.

This study's objectives can be summarized as: 1) to determine primate group densities in each forest type; 2) to quantify forest structure in each forest type by measuring the structural features of trees and vegetation; 3) to distinguish prospective relationships between habitat characteristics and associated primate group densities; and 4) identify how the vegetation characteristics at this disturbed study site compare to expected values of Laumonier's (1997) description of the land units. The field site has been disturbed to a considerable extent due to previous logging activities, but specific areas may have experienced greater habitat disturbances as a result of accessibility. These disturbances are expected to be reflected in habitat structure characteristics

Accordingly, this study's hypotheses are:

1) Land units will show differences in forest structure, which will be measured through: size (DBH); bole height; height; connectivity; branch availability; and tree density. Accessibility of each land unit will have been influenced by topography and the location of areas relative to Sikundur's established trail systems. *Plains* and some of the *Hills* have the most extensive trails, and they are off the main old logging road that runs from the village through the forest. These differences in accessibility are expected to cause differences in forest structure, with the most accessible land units having few large trees, lower tree heights, low connectivity and reduced branch availabilities.

2) There are differences between land units in primate densities with the forests with most stratified structures having the highest primate densities. Stratified, structurally complex, and uninterrupted canopy profiles are more likely to display high group densities of lar gibbons and siamangs since this allows both species to co-exist through niche separation (in 3D space and diet) due to differences in body size and canopy usage. Land units with connective canopies and a high abundance of tall emergent trees will exhibit higher primate group densities because they will facilitate direct route travel, thereby minimizing energy expenditure.

2. BACKGROUND

2.1 Forests and Primate Communities

Forests are terrestrial ecosystems that perform a multitude of life-sustaining ecological services, such as climate regulation and carbon storage. Within the forest, trees are the individual units and their functional importance is multifaceted. For example, trees can serve as shelter from the weather, provide food resources, function as sleeping sites, or provide pathways for travelling (Paciulli 2010). As a whole, the forest plays an active role in maintaining biological diversity and supporting various life forms such as vertebrates, invertebrates, plants, bacteria or fungi. Tropical forests maintain high biological diversity by providing numerous microhabitats within which organisms can create their own niche space (Raemaekers et al. 1980). Sympatric primate species coexist within the same arboreal environment by distributing their daily activities, such as feeding or travelling, across different canopy layers and time periods. These subtle differences in resource and substrate use, time-allocation and modes of locomotion across the primate order reduces resource competition and promotes niche separation amongst sympatric species (Raemaekers et al. 1980; Cannon and Leighton 2004; Reed and Bidner 2004). Amongst the vertebrate community, primates represent a large component of forests' frugivore-folivore biomass (Chapman et al. 2004) and subsequently play important roles in seed dispersal, pollination, and forest regeneration and maintenance (Gupta and Chivers 2004; Wright and Jernvall 2004).

Asian tropical forests are among the richest forests in terms of biodiversity and endemism (Woodruff 2010). Asian primate communities are mainly distributed across southwestern and southeastern Asia, however, some primate communities are found across China, Japan, and the Philippine Islands (Reed and Bidner 2004). Asian primate communities have a relatively high percentage of species in the 5-10 kg range, few frugivorous species and low population densities of larger species compared to other regions (Reed and Bidner 2004). Furthermore, primates in Asian communities display a dependence on the distribution of fruits, especially figs (Reed and Bidner 2004). A review by Johns and Skorupa (1987) has shown that larger-bodied primates with a frugivorous feeding strategy are negatively correlated with survival ability and are the most sensitive to forest disturbance. This is of particular concern for Hylobatidae, the gibbons and siamangs. Gibbons and siamangs are medium to large bodied primates with a high fruit-based diet. Furthermore, these primates' life history traits, such as low population densities, long generation times, a delayed onset of sexual maturity and long inter-birth intervals (Yanuar 2009) suggest low recovery potentials (Phoonjampa et al. 2011) for these primates and

reduced abilities to respond demographically to habitat disturbances (O'Brien and Kinnaird 2011; Lee et al. 2014). Accordingly, these life-history traits combined with the accelerated rates of habitat loss occurring within Southeast Asia emphasize the urgent nature for research to examine these primates' ecologies and their demographic responses to habitat loss and degradation. Unfortunately, a large gap in knowledge regarding these primate species' ecologies continues to exist and few data sets are available to examine their population and demographic trends (O'Brien et al. 2004). An important step in field research is related to quantifying the forest structure of important forest types and identifying whether the presence and/or magnitude of specific structural elements have an influential effect on primate group densities across their ranges. This will help elucidate which structural features forests must have in order to maintain viable populations of gibbons and siamangs.

The focus of many ecological studies, both past and present, has been investigating which factors limit primate population densities across different habitat types, and many have concluded that the availability of preferred food resources is an important limiting variable (Chapman and Chapman 1999; Marshall and Leighton 2006; Marshall et al. 2009). However, a more recent study by Paciulli (2010) showed that Kloss gibbon, *Hylobates klossii*, densities did not change according to the availability of keystone food resources, such as figs (Paciulli 2010). Paciulli (2010) suggests that gibbons' preferred foods do not necessarily limit their densities because they demonstrate the ability to switch their diets to less desirable food items during periods of food scarcity. More recent research on hylobatids has switched the focus towards examining the importance of forest structure characteristics for primate densities and distributions (Muzaffar et al. 2007; Cheyne 2010; Hamard et al. 2010; Paciulli 2010; Phoonjampa et al. 2011; Akers et al. 2013). Unfortunately, these commonly studied vegetation features, such as stand basal area or total stem density, have not provided much insight into the habitat characteristics needed to support hylobatid populations. Thus, more in-depth measurements on habitat and vegetation structures, such as canopy connectivity or canopy gap frequency, may be needed. Accordingly, this study will characterize the canopy structure in different land units used by gibbons and siamangs and will be conducted across a small spatial scale (~5-10km). This will allow comparisons to be made within a species and among subpopulations, since phylogeny will be controlled for (Chapman and Chapman 1999). Furthermore, studies across small spatial scales will also control for unmeasured ecological conditions and parameters between neighbouring populations (Chapman and Chapman 1999).

2.2 Habitat loss

Habitat loss within Southeast Asia is largely an artefact of anthropogenic activities such as logging, encroachment practices, cash crop plantations, and forest fires (Figure 1; Sodhi et al. 2004; Cheyne 2010; Stibig et al 2014). Species diversity and ecological services within this region are being threatened by habitat destruction at twice the rate of other tropical regions and by overexploitation at six times the sustainable rate (Woodruff 2010). Between the years 1990 and 2010, Southeast Asia lost approximately 6.5% of the region's total land area, which is equivalent to a forest cover loss of ~32 Mha (~320 000 km^2) (Stibig et al. 2014). Furthermore, Miettinen et al. (2011) revealed that forest disturbances are concentrated in specific localities within Southeast Asia. The study specifically identified the eastern lowlands of Sumatra and the peat lands of Sarawak, Borneo, within Indonesia as Southeast Asian regions that experienced extreme levels of deforestation between the years 2000 and 2010 (Figure 2; Miettinen et al. 2011).

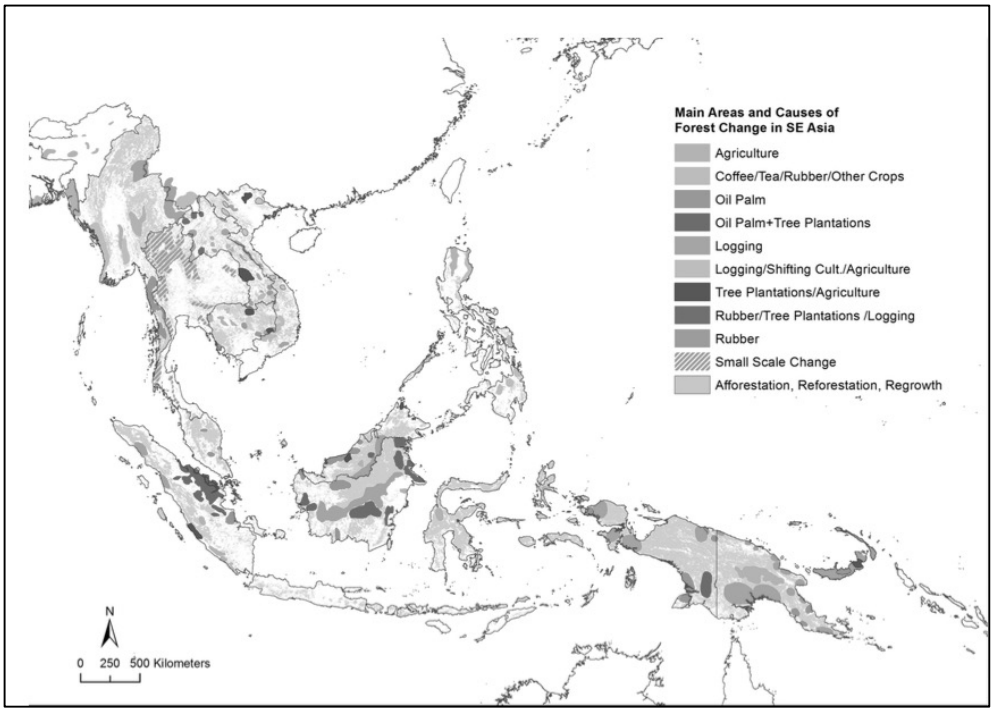

Figure 1. Main areas and patterns of forest-change within Southeast Asia (Stibig et al. 2014)

In addition, the study of Miettinen et al. (2011) also illustrated that specific forest types experienced very high rates of habitat destruction, such as lowland forests, opposed to other forest habitats, such as montane forests. These observed differences are likely related to the accessibility of these forests to commercial activities (Miettinen et al. 2011). Of particular concern with the destruction of these lowland forests is the high biodiversity value they have. Currently, the most significant threats to lowland forests are a combination of expanding palm oil plantations and the creation of road networks required to transport the

palm oil (Gaveau et al. 2009). Most recent research has focused on conserving peat-swamp forests as they are experiencing the highest rates of destruction in both Sumatra and Borneo (Wilcove et al. 2013), however, the lowland forests of Sumatra are also experiencing very high rates of habitat destruction, but remain largely understudied. For example, Gunung Leuser National Park (GLNP) is one of Asia's greatest national parks and has been described as 'one of the largest contiguous expanses of undisturbed rainforest of the western Indo-Malay type in the world' (McCarthy 2000, pp.3). Lowland forests represent 10% of the park's total area and they have the highest biodiversity value of any terrestrial ecosystem (deWilde and Duyfjes 1996), thereby making them valuable study sites. What remains astonishing is the shortage of studies being conducted on lowland forests outside of the Ketambe region (Bowen et al. 2011) within this national park. Hence, this study was carried out at Sikundur Monitoring Post, a field site within Gunung Leuser National Park, on unstudied populations of lar gibbons and siamangs.

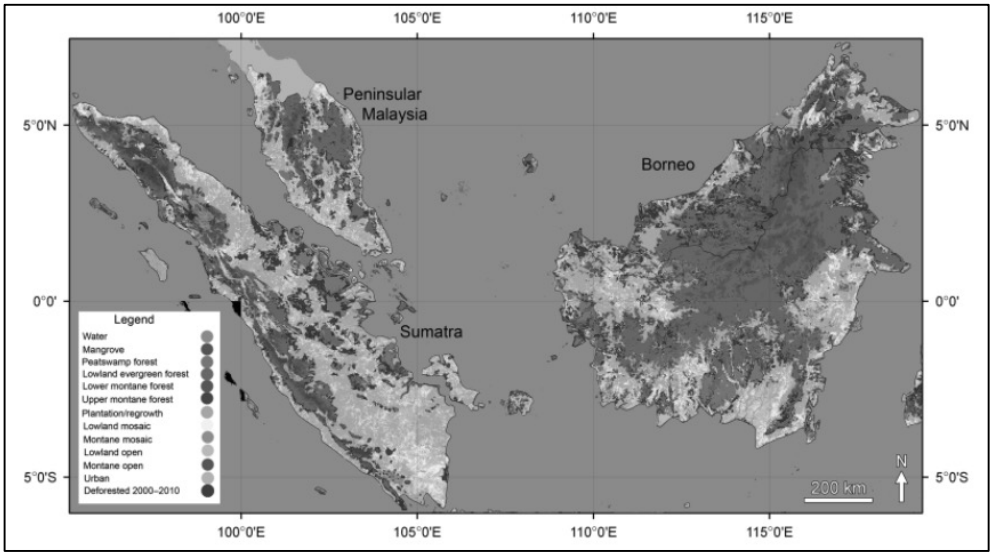

Figure 2. Deforestation in the western part of insular Southeast Asia between 2000 and 2010, with a focus on Sumatra and Borneo islands (Miettinen et al. 2011)

Less than a quarter of Sumatra remains forested (Miettinen et al. 2011). Sumatra's forest loss is a combined result of Indonesia's past logging activities and recent increases in agricultural plantation practices. Within the past decade, a total of 6.2 million hectares of Sumatra's forests have been assigned to oil plantations (YOSL-OIC 2009). Margono et al. (2012) identified that primary forest cover loss in Sumatra totalled 7.54 Mha, with a rate of 0.38 Mha forest lost per year and a rate of forest degradation of 0.12 Mha per year between 1990 and 2010 (based on Landsat data). Furthermore, 47% of the 1990 Sumatran primary forest was degraded or cleared during the study period (Figure 3).

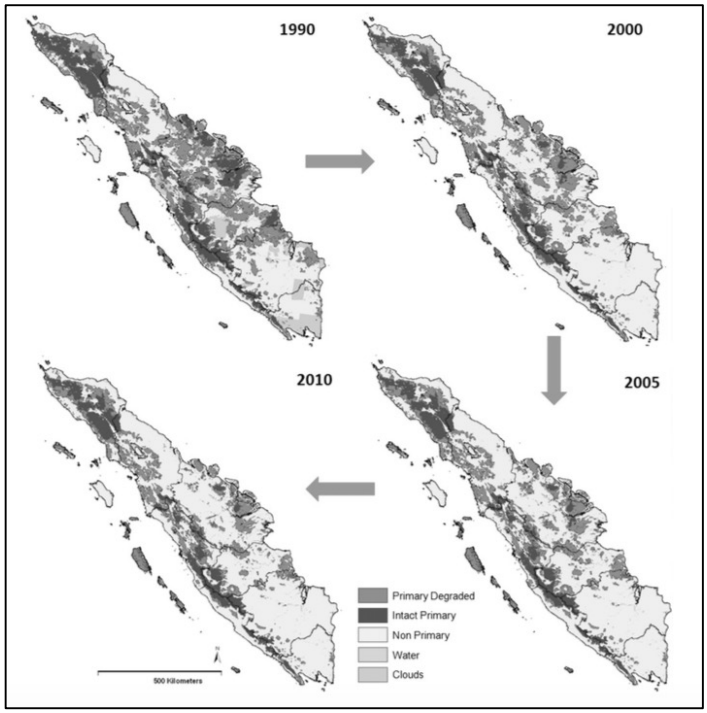

Figure 3. Sumatra's primary forest cover change between 1990-2010 (Margono et al. 2012)

Despite the negative impacts of plantations on forest habitats and wildlife, the use of agricultural plantations has increased between 2000 and 2010 because of the supported idea that the use of palm oil as biofuel will reduce fossil fuel emissions. However, when land is cleared or burned to create a plantation, a large amount of carbon is released into the atmosphere from forests' natural sources. Thus, biofuel plantations are contributing to the climate change crisis just as fossil fuels do (YOSL-OIC 2009). This has not only accelerated habitat loss, but it also helps illustrate the requirement to employ educated decision makers to implement effective conservation initiatives that will protect forest habitats and species from forest exploitation practices.

A United Nations initiative known as REDD (reduced emissions from deforestation and forest degradation) has been proposed as a financial mechanism to credit developing countries for their actions towards reducing deforestation (Miles and Kapos 2008). A study by Gaveau et al. (2009) developed predictive models that estimated the amount of deforestation that would or would not occur if REDD interventions were put in place as a response to the actions of the Indonesian Government for planned extensions of road networks throughout the interior of North Sumatra (Gaveau et al. 2009) The worst case scenario would be one without any REDD interventions and consequently deforestation rates would increase from 294 to 385 km^2 yr^{-1} due to new road construction. Forest cover that was present in 2006 (9226 km^2) would shrink by >25% by 2030 (scenario a). The intermediate

scenario would involve REDD being implemented by establishing a new protected area (PA), but road construction would continue. Accordingly, deforestation rates would decrease from 385 to 329 km^2yr^{-1} because existing and new protected areas would mitigate deforestation. This is represented as a limited conservation success since 1313 km^2 of forest would be saved, but forests outside the protected areas would shrink by 7913 km^2 (scenario b). Lastly, the best-case scenario would involve road construction being halted. Furthermore, REDD payments to communities or oil companies for not clearing forests outside the protected areas would reduce deforestation rates in northern Sumatra from 329 to 58 km^2yr^{-1}. Furthermore, forest cover present in 2006 (1402km^2) would shrink by <4% by 2030, thus this scenario would save an estimated 7824 km^2 of forested area (scenario c) (Figure 4; Gaveau et al. 2009). Gaveau et al.'s (2009) study demonstrates the significant effects REDD interventions would have towards reducing deforestation rates.

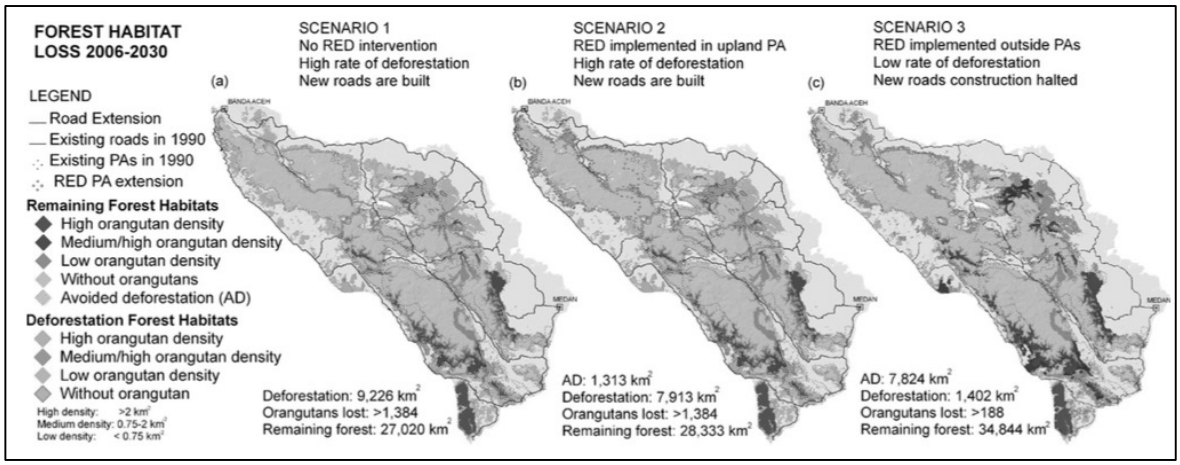

Figure 4. Forest habitat lost to deforestation and forest habitat saved by avoidance of deforestation by three alternative REDD scenarios: a) no REDD interventions b) REDD implemented in new protected area (PA) c) REDD implemented across all forest landscapes (Gaveau et al. 2009)

2.3 Changes in Forest Structure

Over the past few decades, a large majority of forestry research has been related to examining forest exploiting practices, however, there has been an increase in interest to evaluate the changes in stand structure and species compositions of recovering forests. For example, Priatna et al. (2004) examined the recovery of a selectively logged forest in Indonesia 22 years after logging and reported significant changes in tree structure: 67% of trees in the recovering forest were in the small diameter class (10-20 cm) and only two trees (0.2%) had diameters above 100 cm (Priatna et al. 2004). Another study by Okuda et al. (2003) in Malaysia showed that mean canopy height (27.4 m) of the primary forest was

significantly greater than that of the regenerating forest (24.8 m). High canopy trees (>40m) represented 12.8% of trees in the primary forest compared to 1.7% in the regenerating forest (Figure 5). The tallest trees in the primary forest reached heights of 62.6 m, whereas those in the regenerating forest only reached heights of 47 m (Okuda et al. 2003). In addition, Okuda et al. (2003) described a reduction in the complexity and heterogeneity in the canopy surface of the regenerating forest, which further exemplifies the structural changes occurring in regenerating forests.

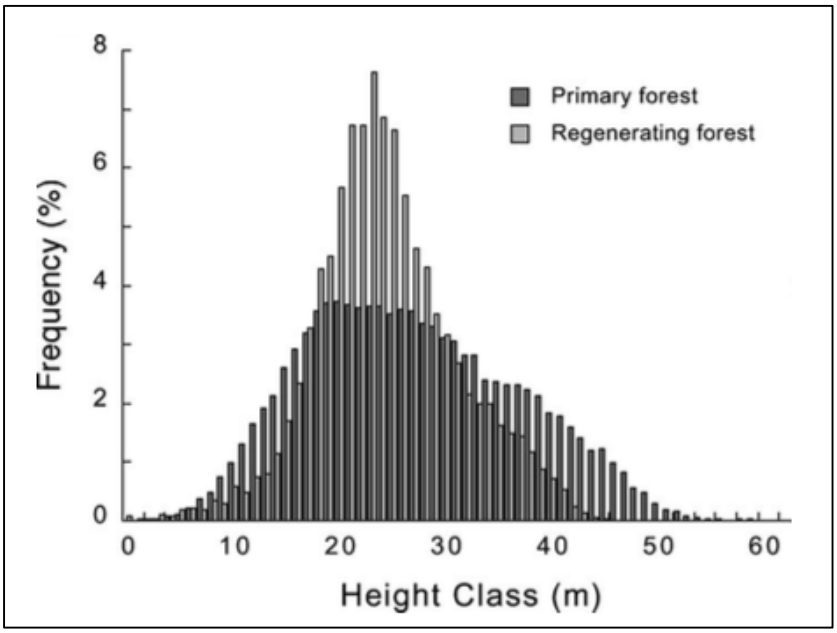

Figure 5. The canopy's height class distributions of a primary forest and regenerating forest (Okuda et al. 2003)

A study by Webb (1997) in Costa Rica showed a significant difference in the median gap size before (46.6 m^2) and after logging (83.5 m^2). Furthermore, prior to logging, 60% of the total gap area was contained in gaps of less than 250 m^2, whereas after logging 78% of the total gap area was accounted for by gaps with an area over 500m^2. Even though very large gaps only accounted for 8% of the gap frequency, they were responsible for occupying 62% of the total gap area (Figure 6; Webb 1997).

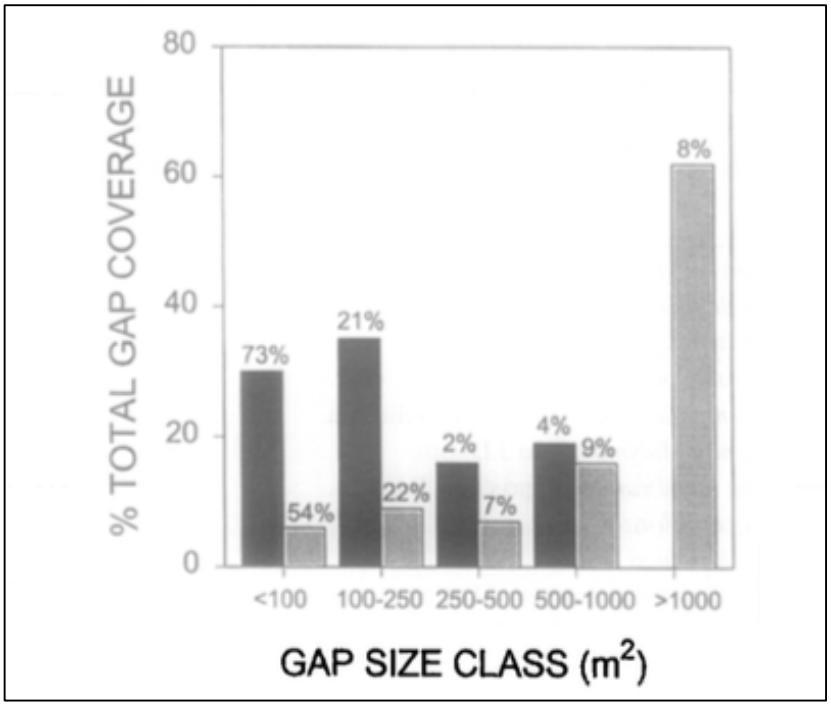

Figure 6. The percentages of total gap coverage for each gap size class. Black bars represent gap size classes before the logging event, whereas post-logging gap sizes are represented by grey bars. The percentages located at the top of each bar is the total proportion of total gap frequency represented by that size class (Webb 1997)

In brief, the survival and persistence of primate populations inhabiting disturbed forests can be challenging because of the structural and compositional changes occurring within recovering forests. Understanding how primate populations are responding to these changes in habitat structure is highly important as studies have identified primate populations sizes to be correlated with forest structure characteristics (Paciulli 2010). Accordingly, this study is concentrating its efforts in comparing the structural elements of forest structure among different land units that have experienced disturbance in the past in order to help clarify if logged or disturbed forests can continue to support viable primate populations.

2.4 Habitat loss effects on primate communities and individuals

The effects of habitat loss on animal communities within degraded or fragmented forests can be large in magnitude and have long-lasting negative effects. Overall, some common consequences of habitat degradation and forest loss include changes in species richness, species distributions, predator-prey interactions, habitat suitability and increases in disease transmission and parasite loads (Schwitzer et al. 2011). A more detailed look into the effects of habitat loss on animal communities reveals that changes in food distributions or abundance and losses in sleeping trees or hiding places are common consequences.

Furthermore, forest gaps or openings are likely to increase predator-prey interactions and potentially increase human predation pressures (Schwitzer et al. 2011). The effects of habitat loss are not only limited to causing variations in biotic communities, but also extend to causing changes in forests' abiotic characteristics. Fluctuations in abiotic characteristics can lead to changes in forest structure and their microclimates. Consequently, these changes may increase a habitat's vulnerability to natural disasters or exacerbate the effects of natural phenomena, such as seasonal droughts (Schwitzer et al. 2011).

The long-term effects of habitat loss and degradation on animal populations have been a concern for conservationists. Changes in habitat quality affect the ranging behaviours and activity budgets of primates (Johns 1986; Schwitzer et al. 2011). Habitat disturbances are likely to influence the distribution of food resources, especially if they are patchily distributed in the first place. Boyle et al. (2009) and Boyle and Smith (2010) showed that bearded sakis (*Chiropotes* spp.) living in fragmented habitats occupied smaller home ranges, lived in smaller groups, and travelled shorter daily distances than those in larger forested areas (Schwitzer et al. 2011). However, the effects of anthropogenic activities on primate communities may not be immediately detectable, but show a delay and a reduction in reproductive success and can take a while before it leads to observable density differences (Chapman and Lambert 2000). For example, Struhsaker (1976) detected a significant decline in vervet monkey, *Cercopithecus aethiops,* populations after 10 years of disturbance, only when 90% of their major food resources were gone.

The effects of habitat degradation appear to be much more severe for arboreal primates than terrestrial ones. It is likely that arboreal primates' increased vulnerability to habitat degradation is a cumulative effect of multiple characteristics, such as loss of food trees, a higher number of canopy gaps, and impaired locomotion (Phoonjampa et al. 2011). Cant (1992) identified four major habitat-related problems that arboreal primates face: 1) straightening the path of movement; 2) negotiating large supports; 3) crossing gaps between trees; and 4) increasing speed along the path of movement (Manduell et al. 2012). There is a high probability that these habitat-related problems will become intensified or more severe in the presence of habitat disturbance and forest loss.

Gibbons and siamangs must deal with locomotive challenges caused by an increase in gap frequencies or the creation of very wide gaps in disturbed forests. These changes result in an increase in energy expenditure because less direct travel paths remain available and they are limited in the distances they can cross with brachiation (Cheyne 2011; Cheyne et al. 2013). For example, Engstrom (2000) showed that orang-utan, *Pongo pygmaeus,* densities were reduced in disturbed forests with high gap frequencies, which may be a result of an increase in energy demands experienced by the orang-utans in order to reach more

dispersed food resources (Cheyne 2011). Nijman (2001) showed that gibbons in disturbed habitats shifted their activities from the upper canopy to the middle canopy (Figure 7) and they increased the proportion of time resting and decreased the proportion of time participating in conspicuous activities, such as singing, feeding or travelling (Figure 8; Johns 1986; Nijman 2001). Furthermore, in disturbed habitats, gibbons increased freezing behaviours and reduced fleeing noisily in response to human presence (Nijman 2001).

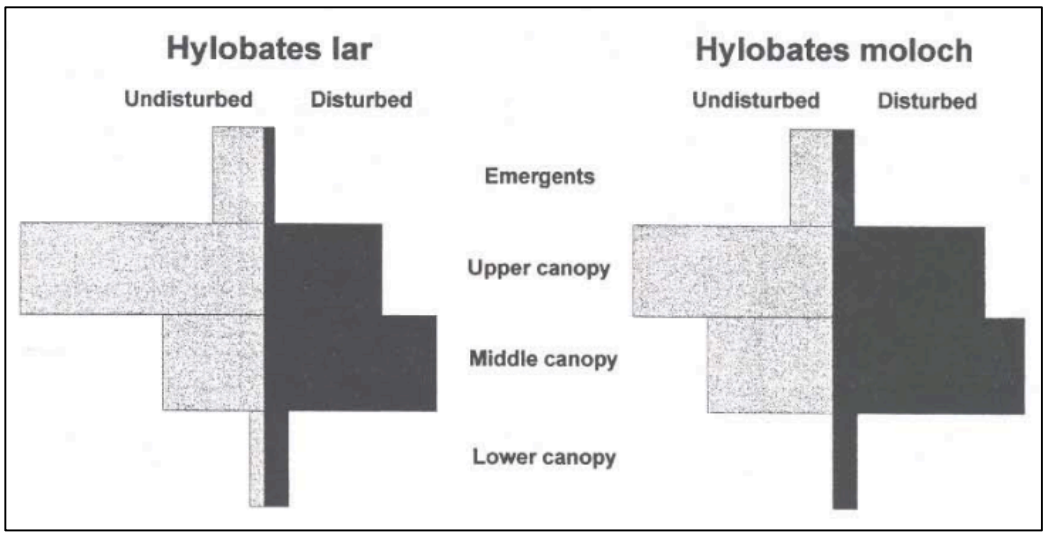

Figure 7. The distribution of gibbon activities in each canopy layer between undisturbed and disturbed habitats (Nijman 2001).

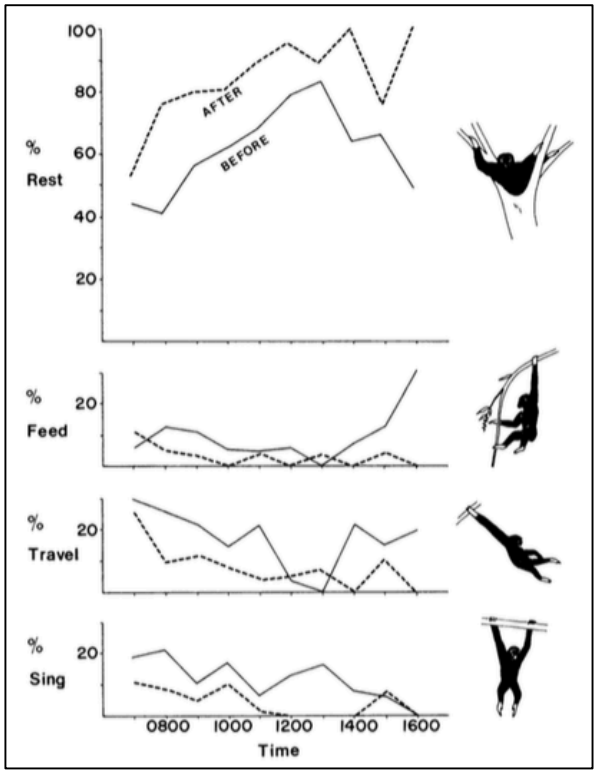

Figure 8. Changes in activity patterns of *Hylobates lar* before and after logging events (Johns 1986).

Other important consequences of habitat disturbance on gibbon populations include lower fecundity or higher mortality, the latter likely a result of an increase in hunting (Nijman 2001). Similarly, siamang groups in disturbed (burned) habitats have reduced reproductive success in degraded (burned) habitats compared with those occupying non-degraded habitats (O'Brien et al. 2003). Due to their arboreal lifestyles, these primates may encounter obstacles in moving amongst forest patches in degraded habitats with discontinuous canopies and large gaps leading to larger group sizes, a delayed dispersal in sub-adults and a temporary increase in primate densities in disturbed areas (Nijman 2001). Lastly, habitat disturbances are likely to cause shifts in the distributions and abundances of food resources, specifically fruit trees, which will impact gibbons' and siamangs' feeding strategies. Gibbons and siamangs may switch to a more folivorous diet when fruit resources are less abundant or more patchily distributed (Johns 1986; O'Brien et al. 2003).

Throughout this review on habitat loss and its effects on primate communities, important changes in both the behaviours and ecologies of gibbons and siamangs have been discussed. The general responses of these primates have been used for comparative purposes and to illustrate trends, however, these changes may not be true or uniform for all hylobatid populations. Chapman et al. (2000) advise that the applicability of a study's general results from one field site to another is limited in its usefulness as variability in factors (i.e.

methodology, site history, environmental factors etc) amongst sites can produce divergent results. This is especially important for this study as it emphasizes the importance of obtaining original data on the primate populations from Sikundur in Gunung Leuser National Park, even though numerous studies have been conducted on gibbons in Ketambe and siamangs in Malaysia.

2.5 Conclusion

At the present moment, data is lacking in providing a valid explanation as to why gibbon and siamang densities vary across forest habitats with varying vegetative and structural characteristics. The majority of gibbon studies have focused on behavioural aspects, whilst very few have provided important information on gibbons' habitat requirements and demographic trends. Primatologists have started to cross-examine primate populations and their associative activity patterns in various habitats in an attempt to define forest variables that influence arboreal primates' survival. Lastly, there is an absence of data for gibbons and siamangs outside the Ketambe region within the Leuser ecosystem, thus original research at new field sites is a key step that will help fill in knowledge gaps and lead to informed conservation strategies to be implemented to conserve remaining hylobatid species.

3. METHODOLOGY

3.1 Study Species

Gibbons are small-sized apes classified under the superfamily Homonoidea and are members of the family Hylobatidae (Bartlett 2007). There are four genera of gibbons: *Hoolock* (hoolock gibbon), *Hylobates* (lar group, dwarf gibbons), *Nomascus* (crested gibbons) and *Symphalangus* (siamangs) (Bartlett 2007; Geissmann 2014) and at least 12 recognized species (Bartlett 2007; Cheyne 2010). All gibbon populations are distributed within eastern and southeastern Asia. This study was conducted on lar gibbons and siamangs and for ease of reference this paper will refer to *Hylobates lar* as lar gibbons or just gibbons and *Symphalangus syndactylus* as siamangs. Lar gibbons, also known as white-handed gibbons, exhibit the broadest north to south distributions of all gibbon species (Bartlett 2007). Siamang distributions are more restricted since they are only found on Sumatra, Indonesia and on the Malay Peninsula in Malaysia and Thailand (Gron 2008). Most gibbon species are allopatrically distributed, however, siamangs and lar gibbons exist sympatrically in northern Sumatra (Figure 9; Bartlett 2007; Cheyne 2010). There are two recognized siamang subspecies: *Symphalangus syndactylus* confined to Sumatra and *Symphalangus continentis* of Malaysia (Gron 2008).

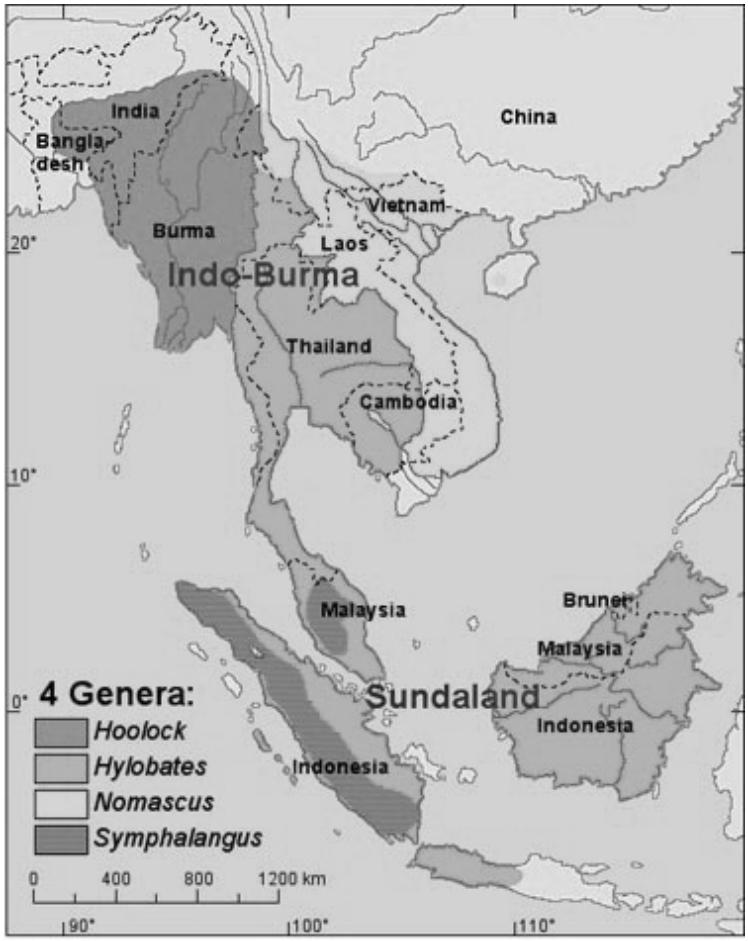

Figure 9. The distribution of hylobatids. Lar gibbons (*Hylobates lar*) and siamangs (*Symphalangus syndactylus*) are sympatric in northern Sumatra (Geissmann 2014)

3.1.1 Physical Characteristics

Siamangs are the largest living hylobatid species (Gittins and Raemaekers 1980; Malone and Fuente 2009), with an adult weighing approximately 10-12 kg. Males and females are similar in size and in colour. All siamangs have black pelage, except around the mouth where the hair is lighter and sometimes takes on a brown coloration (Gittins and Raemaekers 1980; Ankel-Simons 2007). Both sexes have large, naked air sacs in the throat region. These throat sacs inflate when chorusing and function as sound resonators (Gittins and Raemaekers 1980; Ankel-Simmons 2006).

The lar gibbon is much smaller than the siamang, with an average adult weighing approximately 5-6 kg. Lar gibbons vary in coat colour, ranging from a black-like coloration to a fair blonde. All lar gibbons demonstrate two defining physical characteristics: a white coat of hair on both their hands and feet and a white-ring of fur surrounding their faces (Gittins and Raemaekers 1980; Figure 10)

Figure 10. On the left is a picture of siamangs (*Symphalangus syndactylus*) with their inflated throat sacs and on the right is a lar gibbon (*Hylobates lar*) (Geissmann 2014)

3.1.2 Ecology

Lar gibbons and siamangs live in lowland dipterocarp forests and hill dipterocarp forests, but are also found in primary lowland forests, submontane rainforests, seasonal evergreen forests and peat-swamp forests (Gron 2010). Lar gibbons do not typically inhabit forests located above 1200 m, whilst siamangs are found at higher elevations normally inhabiting forests located above 300 m. Thus, the primary habitat type for siamangs is tropical hill forest (Gron 2008), however siamangs also inhabit primary and secondary lowland forest types, as well as primary submontane forests (Gron 2008; Malone and Fiemte 2009)

Lar gibbons and siamangs exist sympatrically in northern Sumatra even though both species have adapted similar locomotive strategies and exploit similar feeding niches. They utilize the stratified canopy using similar strategies. Past studies have consistently observed both primate species engaging in specific activities across different canopy heights. For example, both species normally sing and sleep in the high canopies of emergent trees, but travel and feed in the middle or upper canopies (Gittins and Raemaekers 1980). However, siamangs generally carry out all activities at greater heights than the smaller gibbons. This may be a consequence of their larger body size and/or their tendency to eat a more folivorous diet, which results in them feeding in larger trees with larger supports or on the leaves from tall trees, such as the food tree that grows the fruit durian, *Durio singaporensis* (Gittins and Raemaekers 1980).

Lar gibbons' home ranges are typically larger than those of siamangs (Gittins and Raemaekers 1980). The average home range size for a lar gibbon is 40 ha, whereas that of a

siamang group is 26 ha (Bartlett 2007). These primates' ranging behaviours are governed by the distribution patterns of their food sources (Bartlett 2007; Gron 2010). Within each home range, lar gibbons and siamangs defend a territory against intruders from neighbouring groups. The average territory size of the lar gibbon is 76% (29 ha), and the siamang's is 79% (18 ha) of its home range size (Bartlett 2007). Lar gibbons utilize smaller and more widely dispersed food resources and on average travel 1.4 km each day (Gittins and Raemaekers 1980; MacKinnon and MacKinnon 1980). On the other hand, siamangs concentrate their daily activities to specific regions within their home ranges, leading to travel distances of 1 km or less each day (Table 1). Travel constitutes a larger portion of daily activity budgets in lar gibbons than siamangs, whereas siamangs spend relatively more time feeding (Palombit 1997). Both species devote almost half of their daily activity budgets to resting. Furthermore, lar gibbons and siamangs invest 4-5% of their daily activities to maintain pair bonds and in behaviours related to territory defence, such as intergroup interactions (Figure 11; Palombit 1997).

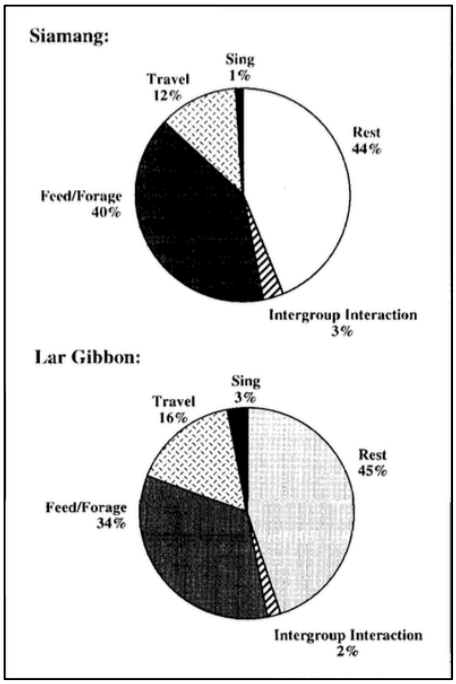

Figure 11. Daily activity budgets of a siamang and lar gibbon in Ketambe (Palombit 1997).

Table 1 Ranging parameters of lar gibbons (*Hylobates lar)* and siamangs (*Symphalangus syndactylus)*

Species	Range Use		
	Day Range (KM)	Home Range (HA)	Territory (HA, %[1])
Hylobates lar	1.4	40	29 (76)
Symphalangus syndactylus	0.8	26	18 (79)

[1]Percent of home range; Table adapted from Bartlett (2007)

3.1.3 Food

Both gibbons and siamangs have a fruit-based diet that is largely composed of figs (Bartlett 2007; Gron 2010), but siamangs tend to be more folivorous and eat less non-fig fruits (Gittins and Raemaekers 1980), which is possible because of their longer digestive tract due to their larger body size (Geissmann 2014). Palombit (1997), in Ketambe found that figs constituted almost half of both species' diets, but the lar gibbon fed more on fruit (71%) than the siamang (61%; Figure 12). Lar gibbons and siamangs are also known to complement their fruit-based diet with young leaves, flowers, and sometimes insects (McConkey et al. 2003; Bartlett 2007; Cheyne 2010). Fruit species from the families *Annonaceae* and *Moraceae* are important food sources for gibbons, which may also be the case for siamangs. These tree species provide primates with fruit nearly all year round due to their asynchronous fruiting cycle (Cheyne and Sinta 2006; Cheyne 2010).

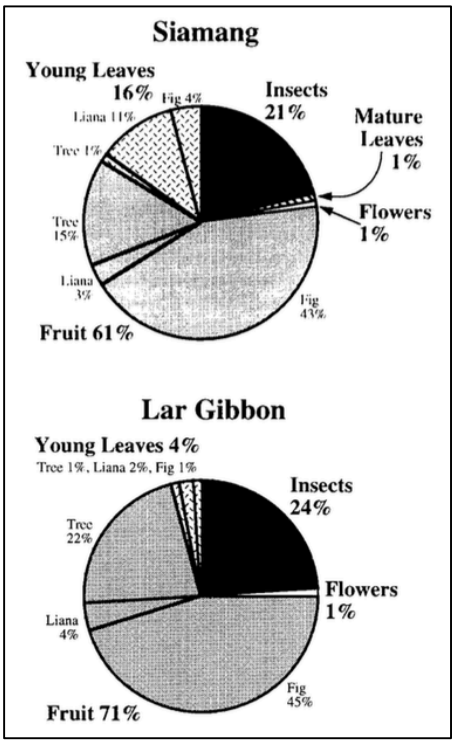

Figure 12. Feeding differences for lar gibbons and siamangs in Ketambe (Palombit 1997).

3.1.4 Locomotion and Morphological Adaptations

Lar gibbons and siamangs exhibit a unique set of morphological adaptations associated with their specialized form of locomotion: brachiation. Brachiation is a form of suspensory locomotion dependent on pendulum-like swings through forest canopies while 'exchanging handholds' (Figure 13; Cheyne 2011). Lar gibbons and siamangs travel across continuous canopies amongst neighbouring trees using cross branch movements and by distributing their body weight on branches relatively far apart (Geissmann 2014; Cheyne 2011). Benefits arising from this type of locomotion include reductions in trip distances, as well as reduced predation risks from their main predators, such as felids, since these primates avoid descending to the ground (Parsons and Taylor 1977). In addition, their locomotive repertoire allows them to access fruit and leaves on the thin, outer branches of trees. This ecological niche is described as the 'terminal branch niche' and remains unavailable to most competitors, thereby reducing feeding competition for these primates (Geissmann 2014). In order to take full advantage of the terminal branch niche, hylobatids have specialized their locomotive repertoire in two ways: brachiation and bipedalism (Geissmann 2014). Bipedalism accounts for 10% of hylobatids' locomotive repertoire (Geissmann 2014) and it occurs usually on large horizontal boughs (Fleagle 1980).

Figure 13. Lar gibbon (*H. lar*): Slow brachiation (after a photo series in Eimerl & DeVore, 1969, pp. 72-73). (Geissmann 2014)

Morphological adaptations for brachiation include elongated forelimbs, a rigid ribcage, highly mobile wrist, shoulder and elbow joints, and a short and inflexible lower spine (Cheyne 2011). Furthermore, their hands and feet are long and slender with four fingers, which act as hooks while grasping tree structures, such as branches (Cheyne 2011). The first digit on their hands and feet are long and separated from the palmar or plantar area (Figure 14; Geissmann 2014) Successful movements through canopies are also dependent on the positioning of the thumbs, which need to be folded and kept out of the way during locomotion (Cheyne 2011).

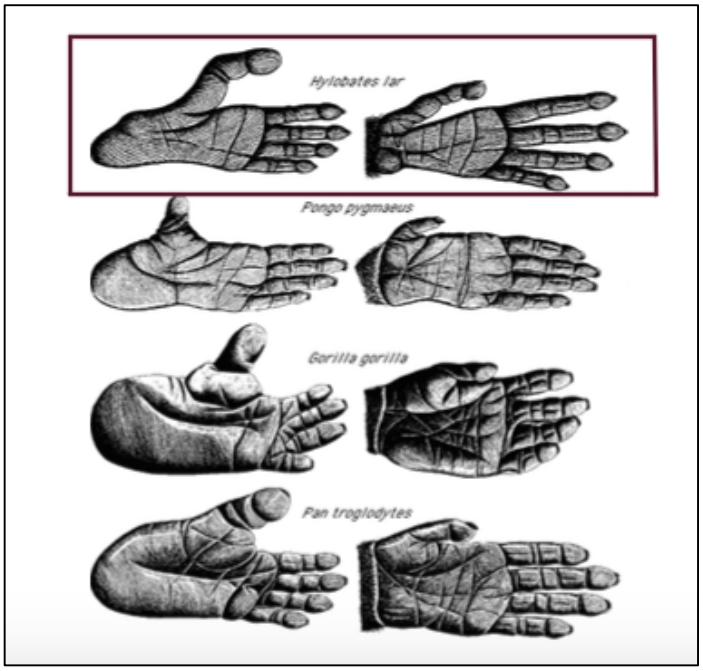

Figure 14. Feet and hands of Hominoidea members (after Beigert, 1963, pp.3/261, 268, 280, and Beigert, 1973, p.171) (Figure adapted from Geissmann 2014)

3.1.5 Vocalizations

Lar gibbons and siamangs are easily recognized from their morning vocalizations. Male and female vocalizations are combined to produce elaborate duets and a critical element to these duets is the coordination of the sex-specific calling phrases (Geissmann 2014). Song duets are typically sung in the early mornings, however calling peaks can differ between species and sexes (Geissmann 2014). For example, at two study sites in Malaysia where siamangs and lar gibbons occurred sympatrically, siamangs' calling peaked approximately 2 hours after that of the lar gibbons (Figure 15). Calls are exchanged between the two adults forming a stable pair and can serve a dual function of strengthening a pair's bond and acting as a mechanism of territorial defence (Bartlett 2007; Cheyne 2010). These primates' songs can be heard as far as one kilometre away and can last for half an hour (Bartlett 2007; Cheyne 2010).

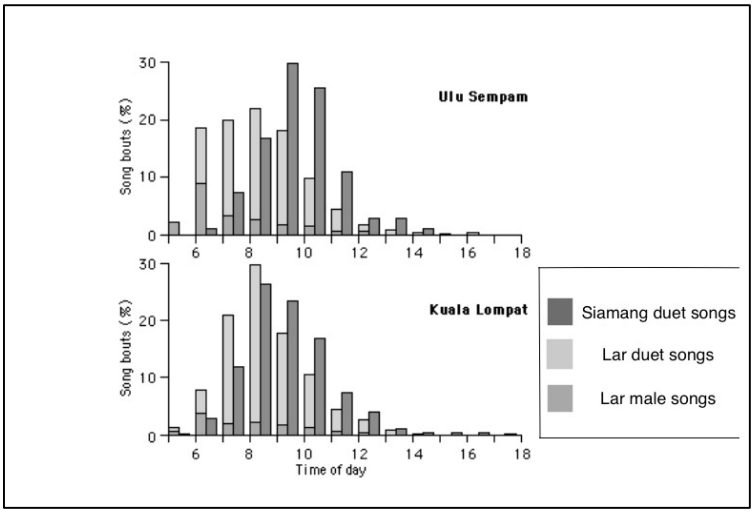

Figure 15. Daily calling patterns of siamangs and lar gibbons at two different study sites in Malaysia (Figure adapted from Geissmann 2014).

There is a notable difference between the songs of lar gibbons and siamangs, however the basic structure and sequence of songs are similar. The structure of a song includes an introductory sequence, a female's great call and the male's reply (Bartlett 2007). The female's great call is highly distinctive with a loud peak note located in the middle of the sequence, whereas the male song, also known as a coda, consists of 'short notes in rapid succession' (Cheyne 2010). Juveniles or immature offspring remain silent during morning vocalizations (Bartlett 2007), however juveniles and sub-adult females may be heard on occasion practicing in tandem with the adult female (Cheyne 2010).

3.2 Field Site

3.2.1 Study Area

The study was conducted at Sikundur Monitoring Post, which is located in the Langkat district of North Sumatra, within Gunung Leuser National Park (GLNP) (04°58'- 04°59' N and 98°04'- 98°05' E) (Figure 16; Nowak 2015). GLNP is located in the Leuser Ecosystem of northern Sumatra, which was first established in 1995 as a conservation area with prospects of conserving rainforest land that could host viable populations of wildlife species (van Schaik et al. 2001). GLNP extends across 1,094,692 ha and provides the last remaining habitat available where four critically endangered species (the Sumatran elephant, orang-utan, rhinoceros, and tiger) co-exist (YOSL-OIC 2009). GLNP is valued as an important national park within Southeast Asia and thus in 2004, alongside Kerinci Seblat and Bukit Barisan Selatan National Park, GLNP was inscribed in the World Heritage List as the Cluster Tropical Rainforest Heritage of Sumatra (Priatna et al. 2004).

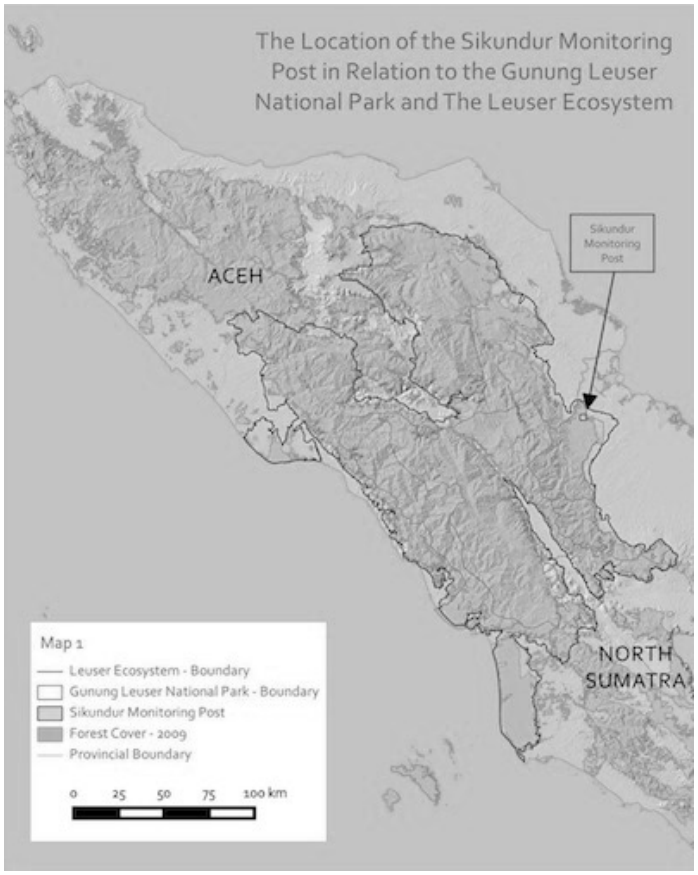

Figure 16. Location of Sikundur Monitoring Post (Nowak 2015).

The Sikundur region, located 30-100 m above sea level (Knop et al. 2004), is described as a mixed lowland dipterocarp forest with rich alluvial forests along rivers (Knop et al. 2004). The landscape varies from gentle rolling hills to steep slopes (Priatna et al. 2004). Recent climatological monitoring at Sikundur Monitoring Post estimated an average annual rainfall of 3,042.8 mm, with the months April-May, September-October and December receiving the highest levels of rainfall. Furthermore, average monthly temperatures at the field site were 27.3°C, with monthly ranges between 26.1-29.2°C (Figure 17; Nowak 2015)

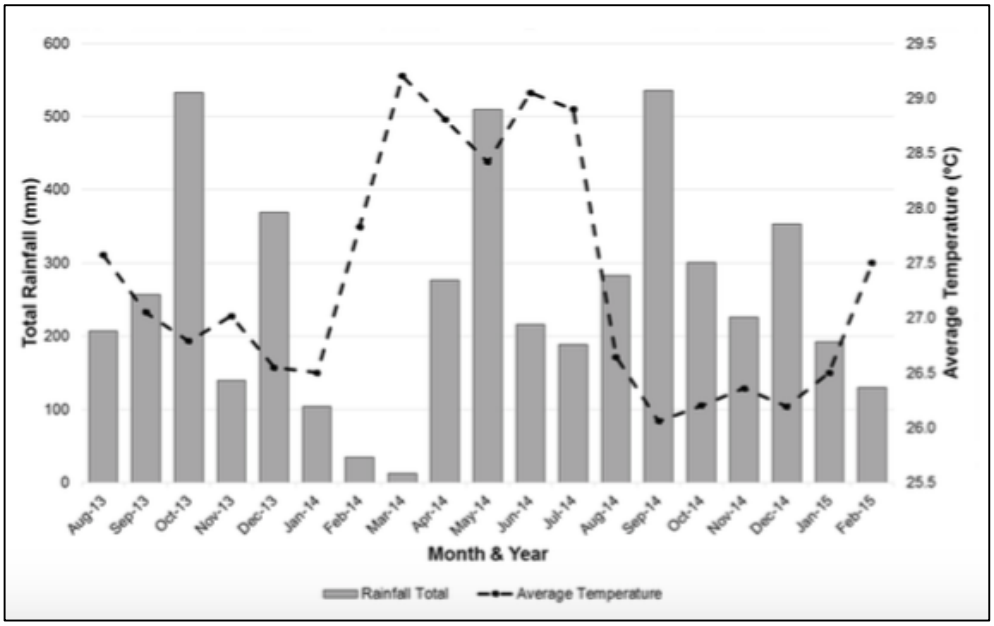

Figure 17. The average temperature and rainfall for the Sikundur Monitoring Post between August 2013 and February 2015 (Nowak 2015).

Sikundur is a unique field site for multiple reasons, including that it is one of the few study sites within Southeast Asia that the siamang and the lar gibbon exist sympatrically. In addition, a study by Laumonier et al. (2010) has demonstrated that different tree flora can exist in forest habitats only a few kilometres apart within Sumatra's lowland forests, even though specific environmental variables, such as elevation, soil type or climate, remained similar or constant. Lastly, an in-depth look into the flora of northern Sumatra has highlighted that the plant communities and species compositions in this region differ distinctly from the rest of the island (deWilde and Duyfjes 1996). These studies illustrate that Sumatra is less homogenous across habitat types and forest compositions as previously thought (Nowak 2015). The implications of this heterogeneity is that the tall lowland forests of Ketambe can differ greatly in structure and composition from the dry, lowland forests of Sikundur. These differences in forest characteristics will provide important habitat and population data comparisons for gibbon and siamang groups between the two field sites for future studies.

Within the study area, three different land units have been identified within Sikundur's forest (Wahyunto et al. 1990; Laumonier 1997). These land units will be referred to as the *Alluvial, Plains*, and *Hills* land units (Figure 18). The *Alluvial* land unit has flat terrain with some undulating slopes (slopes < 8%). The soil is poorly drained, with medium to moderately coarse texture and is non-toxic (Wahyunto et al. 1990; Laumonier 1997). The *Plains* land unit has differentiated sedimentary rock and the terrain is also described as flat with undulating slopes (slopes < 8%). The soil is fluvial with medium to fine texture, well

drained, and has some toxicity (Wahyunto et al. 1990; Laumonier 1997). Lastly, the *Hills* land unit has elongated ridges with slopes up to 25°. The soil is fine with moderate to strong acidity and it is also well drained (Wahyunto et al. 1990; Laumonier 1997). Table 2 identifies additional differences between these land units in terms of climate, topography, vegetation and disturbance histories. Primate densities and tree measurements were sampled from each of these land units.

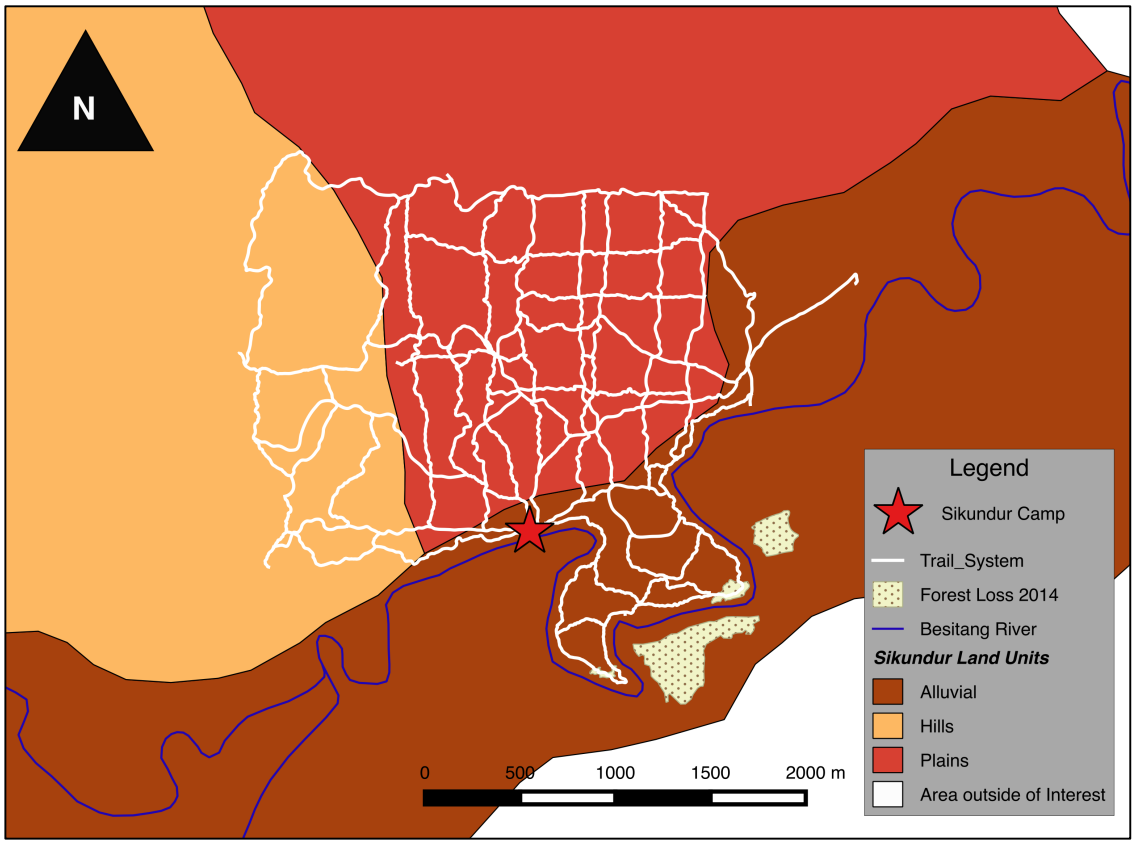

Figure 18. Sikundur Field Site, with different colours distinguishing the land units (Nowak 2015, *pers.comm*).

3.2.2 History of Study Site

The Sikundur region has experienced both small-scale and large-scale logging activities in the past, mainly during the 1960s up until the 1980s, and as a result this conservation area is composed of habitats with diverse disturbance levels (Nowak 2015). However, disturbance is still a problem for areas in the Sikundur area as illegal logging activities and other habitat extractive activities are still occurring (Nowak 2015). The Sumatran Orang-utan Conservation Program (SOCP) has conducted a recent analysis on Langkat District's forest losses and disturbances using data that can be freely downloaded from the Global Forest Watch website (www.globalforestwatch.org; Hammer et al. 2013; Hansen et al. 2013). This

analysis has revealed that a total of 409-forest disturbance 'hotspots' have been identified within the Langkat district between the years 2013 and 2014, (Figure 19) and 94 of these 'hotspots' (23% of all 'hotspots') are located within 10 kilometres of the Sikundur Monitoring Post (Nowak 2015). This new available data helps illustrate the unfortunate circumstances of the local primates occupying Sikundur's forest habitats.

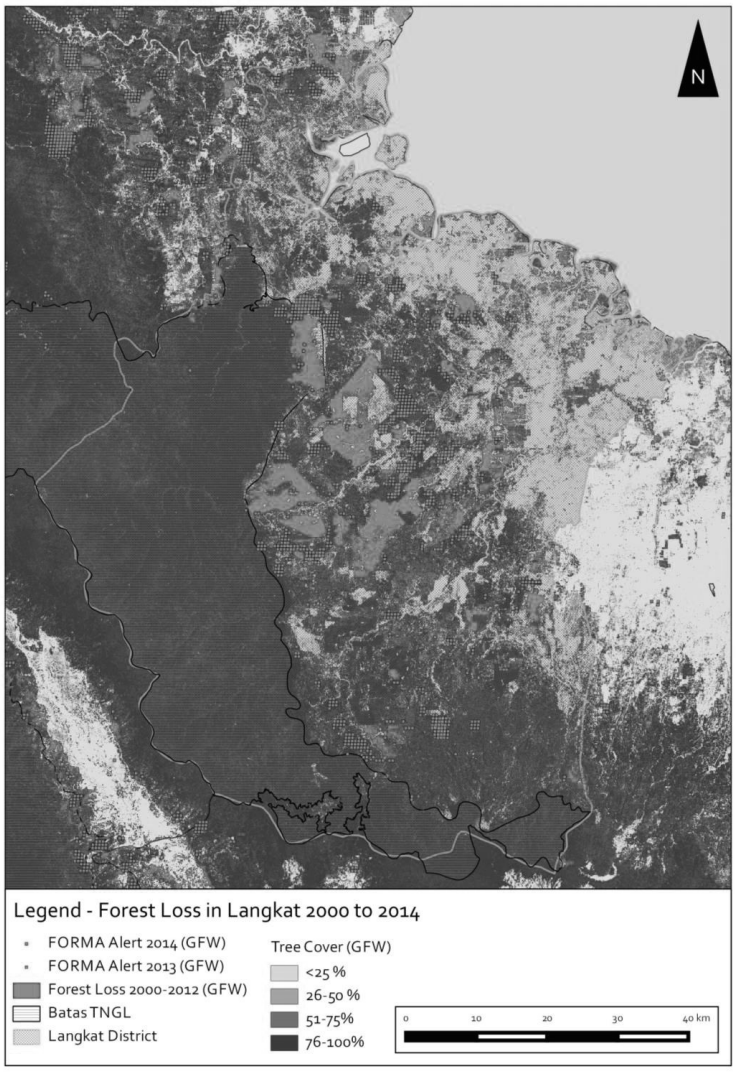

Figure 19. Forest loss in the Langkat district. This data was downloaded from the Global Forest Watch website and analysed by the Sumatran Orang-utan Conservation Program (www.globalforestwatch.org; Hammer et al. 2013; Hansen et al. 2013) (Nowak 2015).

Table 2 Ecological differences between the study site's land units

Land Unit	Climate	Topography	Structure and Floristics	Soil	Disturbance history
Alluvial	Superhumid bioclimate Precipitation between 2000 and 3000 mm/yr	Extend 2 to 5 km inland on either side of rivers Periodically flooded for long periods	Emergent trees reaching 50 m Dipterocarp and palm species Canopy species typically from *Anacardiaceae, Moraceae, Euphorbiaceae*, reaching heights of 20-25 m	Fine texture with high C/N and organic matter content Peat accumulation (<0.5m) occasionally observed	Converted by man due to location near rivers Converted to paddi fields or sago palm
Plains	Superhumid bioclimate Precipitation between 2000 and 3000 mm/yr Eastern edge, especially the South-east, experience dry seasons that can be severe (≤60mm for up to 4 months)	Altitude of 50-100m Terrain is flat to undulating with slopes with inclines from 2-8% and 5-30m in length	Big lianas common Dense undergrowth but herbaceous ground vegetation is sparse Forest canopy varies from 30 to 40m with emergent trees reaching heights of 45 to 55 (60) m. Foliage masses typically found at following heights: 5-10; 15-20; 25-30; and 35-40 m. Dominant species dipterocarps	Drained soils Porous soils with little leaf litter Granular structure and sandy-loamy texture	Extensively logged and replaced by shrubs and grassy secondary vegetation Easily accessed due to abundance of road networks Logging, industrial palm oil, rubber plantations
Hills	Superhumid bioclimate Precipitation between 2500 and 3000 mm/yr Eastern slopes have hyperhumid bioclimate with precipitation between reaching over 3000mm/yr	Low hills reaching altitudes of 500m Crests and summits usually located at altitudes of 450-500m Slopes with inclines ranging from 8-30% Slope lengths range from short to medium (50-150m)	Dense canopy which is well connected Canopy reaching heights of 35 to 40m Emergent trees reaching heights of 45 to 50 m Diversity of tree species very high Dominance of dipterocarp family	Ferralitic soils at low elevations pH of soils between 5 and 6.5, and increases with depth Organic matter ranges from 3-15%	The hills were sparred from the logging operations up until the 80s In the North and South regions of the islands the low hills are almost completely deforested Hills occupied by local villages and influenced by human activities

* Information presented in this table was summarized from Laumonier 1997

3.3 Data Collection

Data was collected between February 4th and June 20th, 2015. Primate densities were calculated using auditory sampling methods or fixed-point counts, whereas forest structure was analysed using vegetation transects and randomly distributed vegetation plots. Designated transects were cut a week prior to sampling in order to ensure primate subjects were not affected by the disturbances (Buckland et al. 2010). The vegetation data collection was conducted by a group of three researchers (John Abernethy, Helen Slater and myself) at the Sikundur field site. In order to reduce inter-observer differences in the vegetation data collection, a pilot data collection was conducted a week prior to the official data collection. The auditory sampling methods required 3 researchers (Supriayudi, Helen Slater and myself) for the data collection. We trained as a group prior to the data collection period to reduce inter-observer bias.

3.3.1 Forest Structure Analysis

Vegetation transects were sampled in order to help determine vegetation differences between each forest type. Furthermore, the use of vegetation plots also provided a point of comparison between the two sampling methods and allowed for a finer scale analysis between forest sites.

Vegetation Transects

Thirty, 500 m transects were evenly distributed across the three land units using a systematic sampling design. All transects were orientated in the north to south direction. A buffer of 100 m was given between consecutive transects in the north and south direction and parallel transects in the west to east direction were 300 m apart. However, due to limited space in the alluvial site, parallel transects were only spaced 250 m apart (Figure 20).

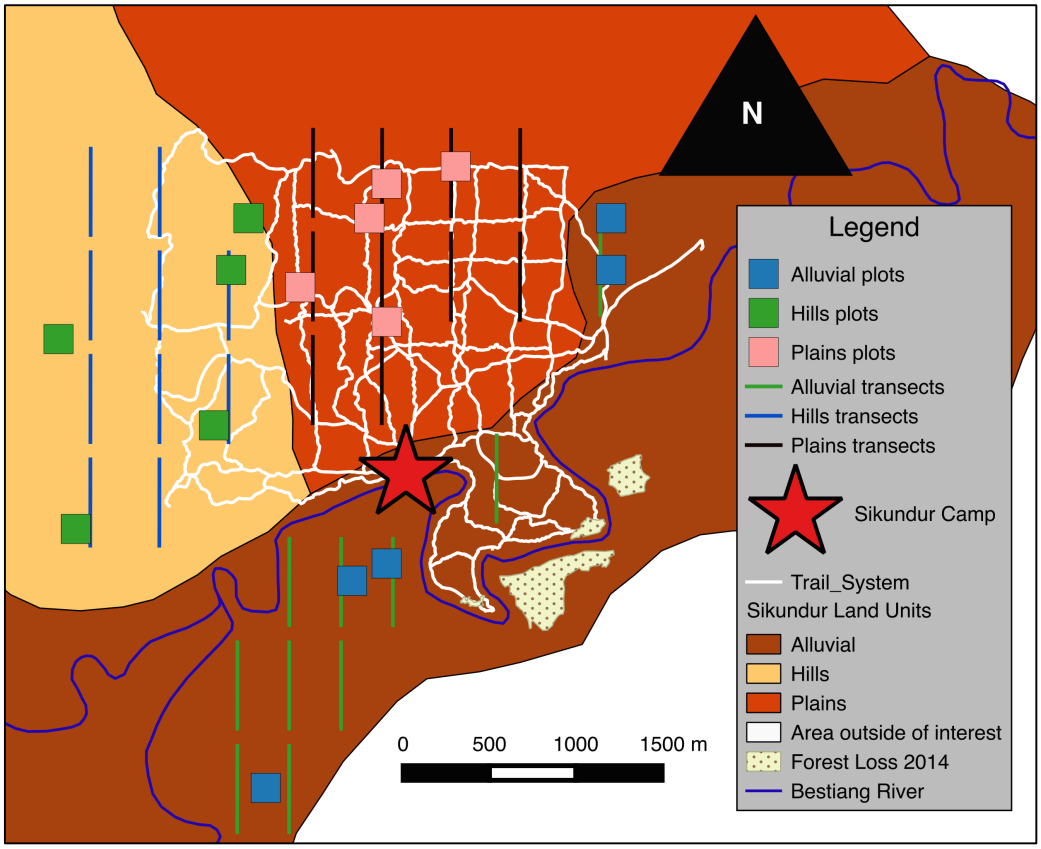

Figure 20. Distribution of vegetation transects and vegetation plots across the study site (Nowak 2015, *pers. comm*).

The 30 vegetation transects were each sampled once and the point-centre-quarter-method (PCQM; Cottam and Curtis 1956) was used to sample the vegetation along each transect. Starting at the 25 m mark along each transect, sample points were taken every 50 m. At each sample point, four quadrants were delineated using a compass' axis (NE, SE, SW, and NW), and the closest tree in each quadrant to the sample point with a diameter at breast height (DBH) ≥ 10 cm was identified. The following 9 variables were measured for the closest tree in each quadrant: *i)* directional bearing of the tree from the sample point; *ii)* distance to the tree from the sample point; *iii)* diameter at breast height (m); *iv)* bole height with a Hawke laser range finder pro 900, i.e. the height of first bough, (m); *v)* tree height with a Hawke laser range finder pro 900 (m); *vi)* crown width – measurements were made from the centre of the tree trunk to the furthest extending edge of the canopy in each compass direction (N, W, S, E) (m); *vii)* branch count for each size category of branch diameter (0-2 cm, 2-4 cm, 4-10 cm, 10-20 cm >20 cm), estimated using the number categories of 1- 10 branches, 11-50, 51-100, 101-500, 501-1000, 1001-5000, 5001-10000, >10000 branches; *viii)* crown shape categorized into one of the shape categories spheroid, elongated spheroid, umbrella, cone, upside-down cone, or bent over; and *ix)* crown connectivity in relation to neighbouring tree crowns. Crown connectivity was measured as

the percentage of the focal tree's crown that overlapped/ touched at least one other tree's crown measured in percentages using a 4-point scale: 0-25%, 25-50%, 50-75% and >75% overlap. Thanks to the broad categories, inter-observer reliability of this measurement was always >90% during the trial period.

Vegetation Plots

Fifteen vegetation plots were randomly distributed across the three land units, with five plots in each site and each plot was sampled once (Figure 20). Each plot was 25 m X 25 m in size and the plots' boundaries were delineated using tape measures, which were laid out on the N-S and W-E axis. For every tree within the plot with a DBH ≥ 10cm, the same sets of measurements were recorded as for PCQM quadrants from the vegetation transects (with the exception of distance and bearing from the sample point as this did not apply with this method).

3.3.2 Primate Group Density Estimates

The line transect technique is the most common survey technique used to estimate primate densities (Nijman and Menken 2005). This technique depends on visually detecting primates on one or both sides of a survey transect (Nijman and Menken 2005). However, this technique has proven to be inefficient in estimating densities for gibbon species because of their elusive and unreliable behaviour in response to human presence (Nijman and Menken 2005; Buckely et al. 2006; Dacier et al. 2011). Accordingly, it has become common practice among primate researchers to use auditory sampling methods to estimate gibbon densities. Auditory sampling uses the vocal repertories amongst gibbon conspecifics to estimate gibbon densities. Auditory sampling is a time-efficient sampling method that allows density estimations of gibbon populations over large sampling areas (O'Brien et al. 2004; Höing et al. 2013). In addition, auditory sampling is applicable over hilly terrain and has no influence on gibbon behaviour (Höing et al. 2013). For these specific reasons, this study used auditory sampling methods to collect primate group density data. In addition, density transect walks were also conducted using established transects lines from vegetation sampling. These transect walks provided supplementary data to the vocal sampling as density transect walks on their own are unlikely to provide reliable primate group estimates for the Sikundur region.

Auditory Sampling

Three vocal sampling points were established within each of the land units. For ease of reference, this study will refer to a set of vocal sampling points as an array. Until recently,

most auditory sampling studies for hylobatids have followed the guidelines provided by Brockelman and Ali (1987), however, a recent study by Kidney et al. (2013) conducted an acoustic simulation study in order to compare auditory sampling survey designs with alternative listening post set-ups (Kidney et al. 2013). This study evaluated the performance of the gibbon density estimator across various listening post arrangements, which included *(i)* 3 by 1 linear; *(ii)* equilateral triangle (used by most studies); *(iii)* 4 by 1 linear; and *(iv)* 2 by 2 square (Kidney et al. 2013). Kidney et al. (2013) concluded that the linear array simulations yielded lower variances than non-linear simulations of the same size. Therefore, this study used a 3 by 1 linear post arrangement (as a 4 by 1 linear post arrangement was not feasible due to limited man-power in the field).

Accordingly, each array had three listening posts arranged in a line with a minimum distance of 500 m between listening posts (Figure 21; Höing et al. 2013; Kidney et al. 2013; Lee et al. 2014) and each array was sampled once over a period of four days. Observers situated themselves at the highest point possible in order to maximize listening quality and accuracy related to determining the direction of each call. For each array, observers were located at each of the three listening posts and data were collected for four consecutive days between 05:00 – 11:30 h, since O'Brien et al. (2004) observed that gibbon calling stabilizes by the fourth day. Researchers recorded both the start and end time of all songs and calculated the length of duets. Compass bearings and estimated distances to calling gibbons and siamangs were also documented (Buckley et al. 2006; Höing et al. 2013). Researchers remained at each listening post until gibbons and siamangs had stopped singing for ≥ 30 minutes (Höing et al. 2013).

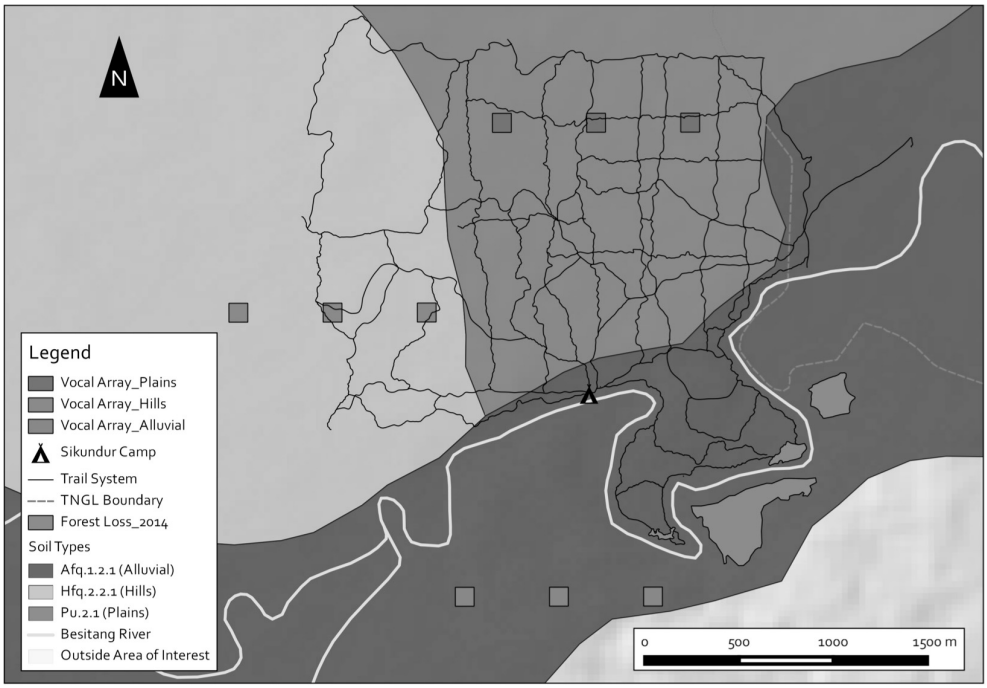

Figure 21. Locations of vocal arrays in each land unit *(Alluvial, Plains*, and *Hills*) (Nowak 2015, *pers.comm*).

Surveys were only conducted during suitable weather conditions, i.e no rain, since calling frequency is affected by weather conditions, such as rain or wind (Nijman and Menken 2005). Differences in detectability between the land units was not a major concern due to the small size of the study site, which resulted in the elevation and terrain level to remain fairly similar between land units.

Density Transects

The established vegetation transects were also used for density walk censuses in order to collect supplementary primate group density data. Density transects rely on the direct observations of animals on one or both sides of the transect path (Nijman 2001), and accordingly can be used to estimate habitat-specific-primate densities (Marshall 2010). Each of the thirty transects were sampled twice, one in the morning and once in the afternoon, thus a total of 60 density transects were walked, totalling 30 km. Morning transects were walked between 07:00 h and 10:00 h and afternoon transects were walked between 15:00 h and 18:00 h. All transects were walked with a team of 2 observers at a regular, steady pace of 0.5-1 km per hour with regular stops made every 10-20 m to take a full 360° look around. With each primate encounter, the following data were recorded: i) GPS coordinates of observer's position along the transect path; ii) directional bearing (angle) of the primate(s) from the transect; iii) primate species; iv) group spread (number of individuals); v) estimated distance to primate(s) from transect by the observer (distance to group centre if >1 primate); vi) height of primate(s) in canopy with a Hawke laser range finder pro 900 (height of group

centre in canopy if >1 primate); vii) detection method (visual or audial); and viii) behavioural activity.

3.4 Data Analysis

3.4.1 Forest Structure Analysis

After tests for differences between sampling methodologies using Mann-Whitney *U* nonparametric tests showed no significant differences (all cases $U > 144000$, $P > 0.05$) in vegetation characteristics between transect and plot data, these data were pooled together and analysed as one data set. Normality tests were conducted on all variables measured and those with non-normal distributions were compared using nonparametric Kruskal-Wallis tests and Mann-Whitney *U* post-hoc tests. Sequential Bonferroni probabilities were used to determine significance levels (Rice 1989). The significance level, α, was divided by the number of tests in a sequential order. First, the *P* values were ranked from smallest to largest. The smallest *P* value was considered first and α was divided by the number of total tests, *k*. If $P_1 \leq \alpha/k$, then the corresponding test indicated significance. If $P_1 \geq \alpha/k$, all tests indicated non-significance and remaining *P*-values were non-significant. If $P_1 \leq \alpha/k$ was met, then the next smallest *P*-value was analysed. If $P_2 \leq \alpha/(k\text{-}1)$, this test also indicated significance. If $P_2 \geq \alpha/(k\text{-}1)$, then this corresponding test and all other tests with larger *P* values indicated non-significance. This method continued until a test indicated non-significance and thus all remaining *P*-values were also non-significant (Rice 1989).

Table 3 illustrates the mid-values used for each branch diameter category class in the Kruskal-Wallis nonparametric tests and Mann-Whitney *U* post-hoc tests (Manduell et al. 2012) in order to compare differences in branch availabilities between the three survey sites. As all variables had non-normal distributions, the median value opposed to the mean was reported for each vegetation variable within each land unit. As a result of the specific methods used to calculate branch availabilities, i.e. using size classes and calculating the average per class, the mean number of branches for each size category, opposed to the median were reported.

For categorical data, such as crown shape and crown connectivity, chi-squared tests were performed in order to detect significant differences between land units. Frequency distributions of trees taller than 25 m were compared between land units using chi-squared tests. This height value of 25 m was chosen because studies by Cannon and Leighton (1994) and Cheyne et al. (2013) suggested that hylobatids displayed a preference for travelling in canopies 21-30 m above the ground, thus the mid-value of this height range was chosen to represent a preferable tree height that gibbons and siamangs would use for various activities.

Lastly, DBH measurements were categorized into specific size classes, which were delineated by explicit DBH ranges. The categorical size classes used were classified as small (10-30 cm); medium (31-60 cm); and large (>60 cm). Chi-squared tests tested for significant differences in the frequency distributions of DBH size classes between land units.

Specific calculations, including tree densities (trees/ha) and stand basal areas (m^2/ha), were calculated using only the vegetation plot data. These calculations were not applicable to the transect data as a defined area of measurement was required and this was provided only by the vegetation plots (25 m X 25 m = 625 m^2). All tests were carried out using Paleontological Statistics Software Package (PAST) v.3.07, with a significance level of $P<0.05$.

Table 3. Categories used to estimate the number of branches in each size class

Categorical Classes for Number of Branches*	Mid-values used in calculations
1-10	5
11-50	30
51-100	75
101-500	300
501-1000	750
1001-5000	3000
5001-10000	7500
10000+	10000

*Scale adapted from methods of Manduell et al. (2012)

3.4.2 Primate Group Density Estimates

Density Transects

No statistical analyses were conducted on density transect data as no gibbon or siamang were encountered using this sampling method.

Standard Triangulation

In each land unit, the total number of individual groups for lar gibbons and siamangs were determined using triangulation methods. Individual calls were mapped by drawing straight lines using estimated compass bearings of each detected group. Groups were identified at the intersection of lines, which originated from different listening posts (Phoonjampa et al. 2011). Points that were mapped more than 500 m apart were identified as individual groups (Buckley et al. 2006; Phoonjampa et al. 2011; Lee et al. 2014). Previous research suggests that 500 m is the approximate width of any given gibbon territory, thus groups calling more

than 500 m away can be distinguished as distinct and separate groups (O'Brien et al. 2004; Buckley et al. 2006; Phoonjampa et al. 2011). A circular listening zone, also known as a buffer, was fitted around the centre point of each array using the software QGIS version 2.8.2-Wien, in order to determine the sampling area of each vocal array. The radius of the buffer was determined by calculating the distance between the centre post and the group mapped furthest away. Due to the small size of the study site, the vocal sampling areas of the arrays included other land units. This was corrected for by reducing the buffer radii's used until sampling areas encapsulated by the circular buffers for each array comprised a minimum of 80% of the focal land unit. Sections of other land units that were still located within the buffer were excluded from the sampling area (Figure 22). Groups that were identified outside of the radius for the focal land unit were removed. Any groups identified inside the radius, but located in different land units were also removed. These groups were not subsequently incorporated into the group recordings of their appropriate focal land unit as this could result in double-counting of groups already recorded at that focal land unit's vocal array. This was a conservative approach for primate group density analyses so that accurate group density estimates were obtained for each land unit. These calculated buffer radii were used in gibbons' and siamangs' Spatially Explicit Capture Recapture (SECR) models to fix the parameter, *mask buffer*. Table 4 summarizes the buffer radii calculated for each land unit using triangulation methods.

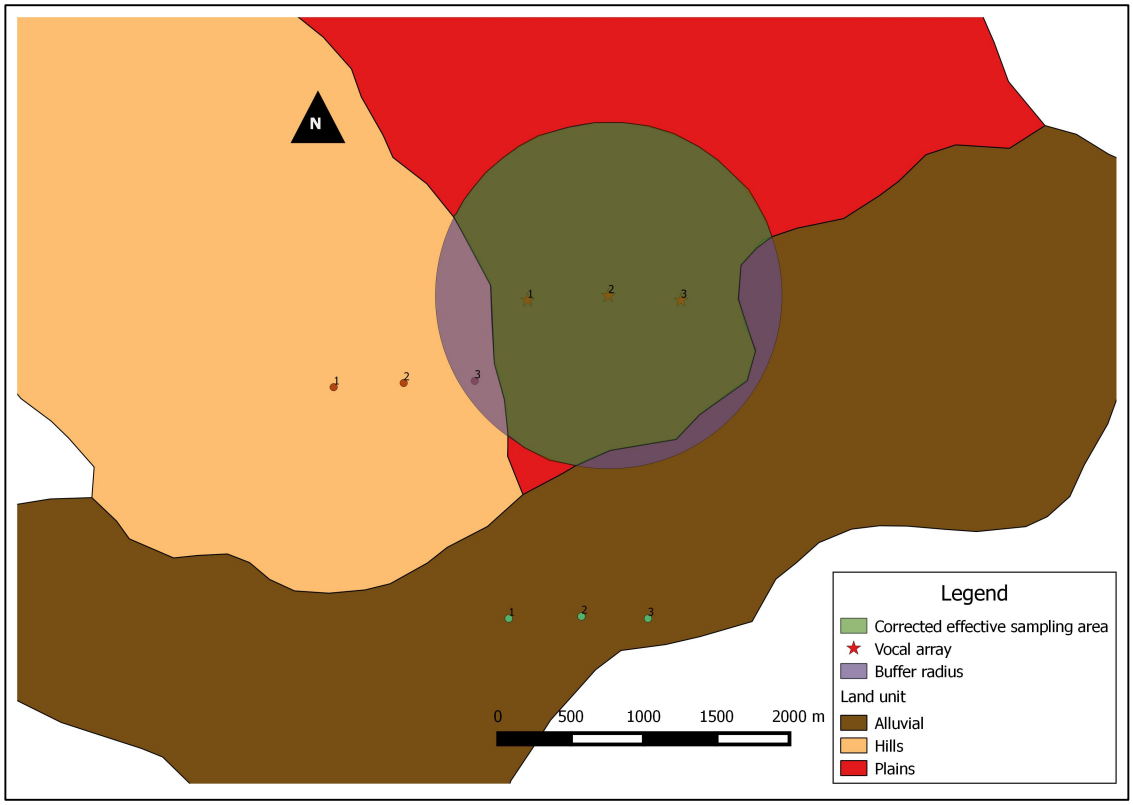

Figure 22. Visual illustration of the method used to calculate buffer radii, using the *Plains* land unit as an example. The purple circle is the circular buffer and the buffer radius has been reduced until 80% of the *Plains*' sample area is encapsulated by the buffer.

Table 4. Buffer radii calculations for each land unit using standard triangulation methods

Land Unit	Original Buffer Radius (km)*	Corrected Buffer Radius (km)	Total Sampling area (km^2)**	Corrected Sampling Area (km^2)***	% of Buffer in Respective Land Unit
Alluvial	1.26	1.0	3.14	2.48	80
Plains	1.19	1.19	4.4	3.77	86
Hills	1.32	1.22	4.65	3.74	80

**For each land unit, the original buffer radius was calculated by determining the distance between the centre post of each array to the group mapped furthers away*
***The total sampling area is the entire area of all land units included in the original buffer*
****The corrected sampling area is the area ONLY of the focal land unit being sampled included inside the corrected buffer. The corrected sampling area does not take into account the areas of other land units that remain inside the buffer.*

SECR Methods

Primate group density estimates were calculated using spatially explicit capture-recapture models (SECR; Kidney et al. 2013). The software package 'gibbonsSECR' was installed into the R program (version 3.1.1) (available at: //github.com/dkidney/gibbonsSECR) and was used to determine density estimates.

Prior to running SECR models, a few parameters were individually fixed as they are species and site specific. First, the calling probabilities for individual gibbon or siamang groups were calculated by dividing the number of days in which each group called by the number of days sampled. For example, if one gibbon group only called on two days out of the four days sampled, this group's calling probability would be 0.5 on any given day. An average calling probability for each species at each land unit was calculated by averaging individual groups' calling probabilities. These averages represented the calling probabilities of the 4-day sample period and were species and site-specific. Accordingly, the average calling probabilities for gibbons and siamangs in each land unit were used to define the model parameter, *calling probability,* in SECR models. Next, the mask buffer is a parameter that defines "the boundary around the listening points beyond which the detection probability is assumed to be 0" (Nowak *pers.comm*). Thus, the parameter, *mask buffer,* was fixed in SECR models using previously calculated site-specific buffer radii. Furthermore, SECR models also used site-specific buffer radii to estimate the effective sampling areas of each vocal array. Lastly, the 'half normal' detection was selected for all SECR models (Figure 23) and this detection function accounts for imperfect detections in the primate group density analyses.

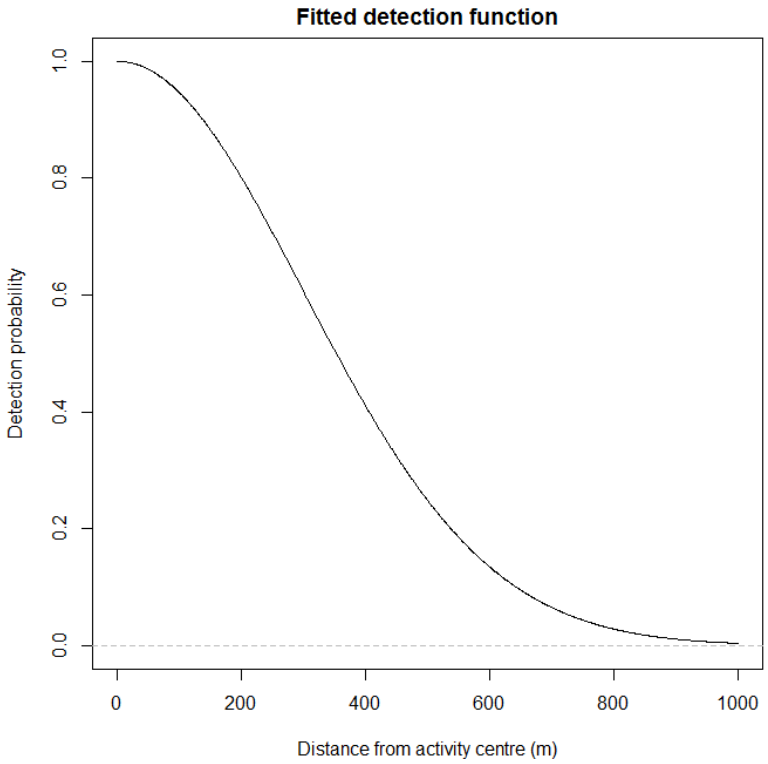

Figure 23. The half normal detection function used in SECR models. This detection function estimates that the probability of detecting a primate call decreases as primate distances from vocal arrays increases. This example detection function graph (showing the results for gibbons in the *Alluvial* land unit) estimates that no calls will be detected when primates are located at distances greater than 1000 m, or 1 km from vocal arrays. Other graphs are presented in Appendix I.

3.4.3. Relationships between gibbon/siamang densities and forest structure

Since the data analyses of gibbon and siamang densities only provided three individual densities for each species, no statistical analyses between densities and forest structure were possible. Consequently, the analyses of results will be of descriptive nature only.

4. RESULTS

4.1 Vegetation Characteristics

A total of 1704 trees were measured across the vegetation transects and vegetation plots. The DBHs of trees in the *Alluvial* forest (*N*=572; $median_{alluvial}$= 17.8cm) were significantly larger than those in the *Hills* (*N*=583; $median_{hills}$=15.6cm; *U* = 140500, *P* = 0.0027) and in the *Plains* (*N*=548; $median_{plains}$=15.9cm; *U* = 149000, *P* = 0.0024; Figure 24), but the *Hills* and *Plains* did not differ from each other (*U* = 159400, *P* =0.95). The *Alluvial* forest type had a significantly higher frequency of medium sized trees, corresponding to DBH measurements between 31-60 cm, than the other two sites (Figure 25; *N*=88; x^2= 6.89, *P*=0.03, df=5).

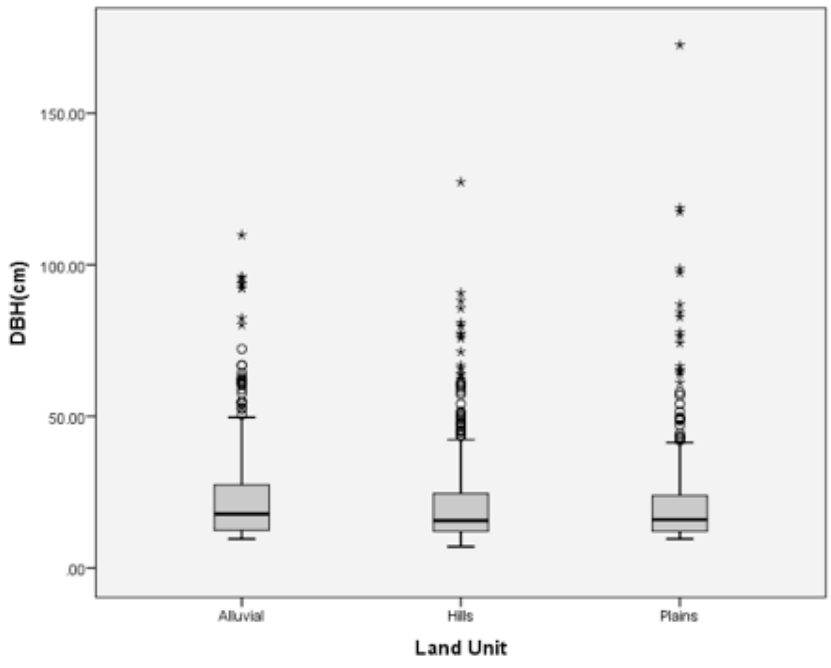

Figure 24. DBH values of trees measured in each land unit; boxes represent quartiles, whiskers represent 95% quartile, * and ° refer to extremes and outliers, respectively.

The tree heights did not differ significantly between the land units (Figure 26; *N*=1704; x^2=3.998; *P*=0.14). The *Hills* (*N*=49; 9% of all trees) and the *Alluvial* forest (*N*=47; 8%) had significantly higher frequencies of trees >25 m than the *Plains* (*N*=27; 5%) site (Figure 27; x^2=8.28; df= 5; *P*=0.015). Bole heights of the *Alluvial* site (*N*=569; $median_{alluvial}$= 8.4 m) were significantly lower than those of the *Hills* (*N*=547; $median_{hills}$= 9.3 m; *U*=143000, *P*=0.014), but no other pair-wise comparisons were significant (N_{plains}= 580; Hills vs. *Plains: U*=148000, *P*=0.03, α'=0.025; *Alluvial* vs. *Plains U*=163000, *P*=0.66).

The *Hills* forest had significantly higher *H:DBH* ratios (N=548; $median_{hills}$=80.73) than the *Plains* (N=582; $median_{plains}$=75.9; U=146900, P=0.0221) and the *Alluvial* land unit (N=571; $median_{alluvial}$=74.8; U=136600, P=0.00023). The median values for all vegetation variables measured in each forest type are summarized in Table 5.

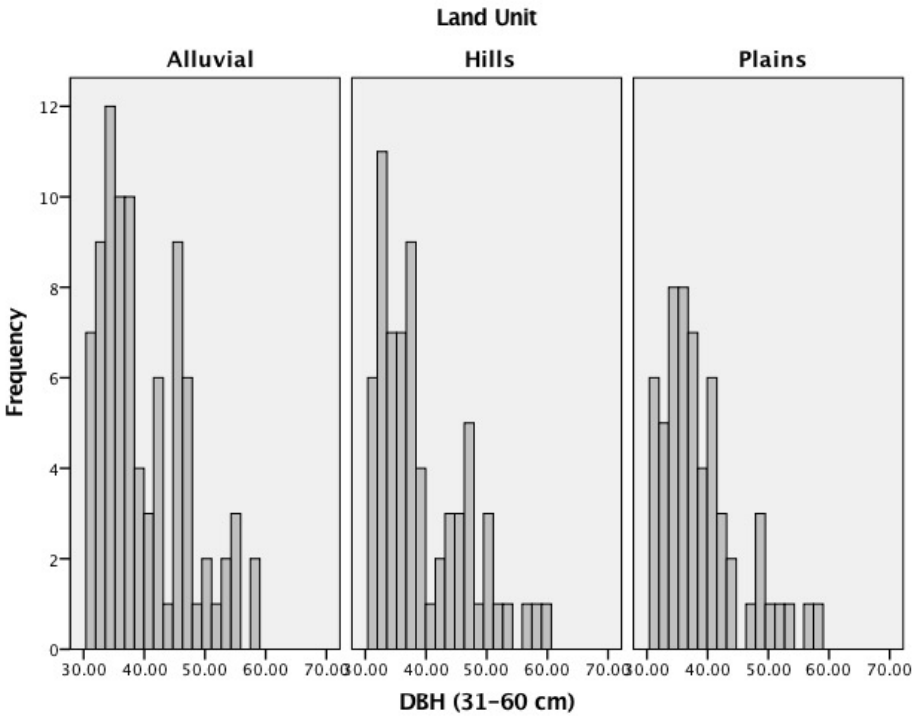

Figure 25. Frequency distributions of DBH measurements for trees with DBH measurements between 31-60 cm.

The *Alluvial* land unit had a greater frequency of larger branches (Table 6; Figure 28) and a greater frequency of having up to 10 branches with diameters of 10-20 cm than the other sites. However, there were no significant differences in the availability of very large supports with diameters > 20 cm between the land units (Table 6).

Canopy connectivity, crown shapes, stand basal areas (SBA), and tree densities did not differ significantly between the land units (Table 5).

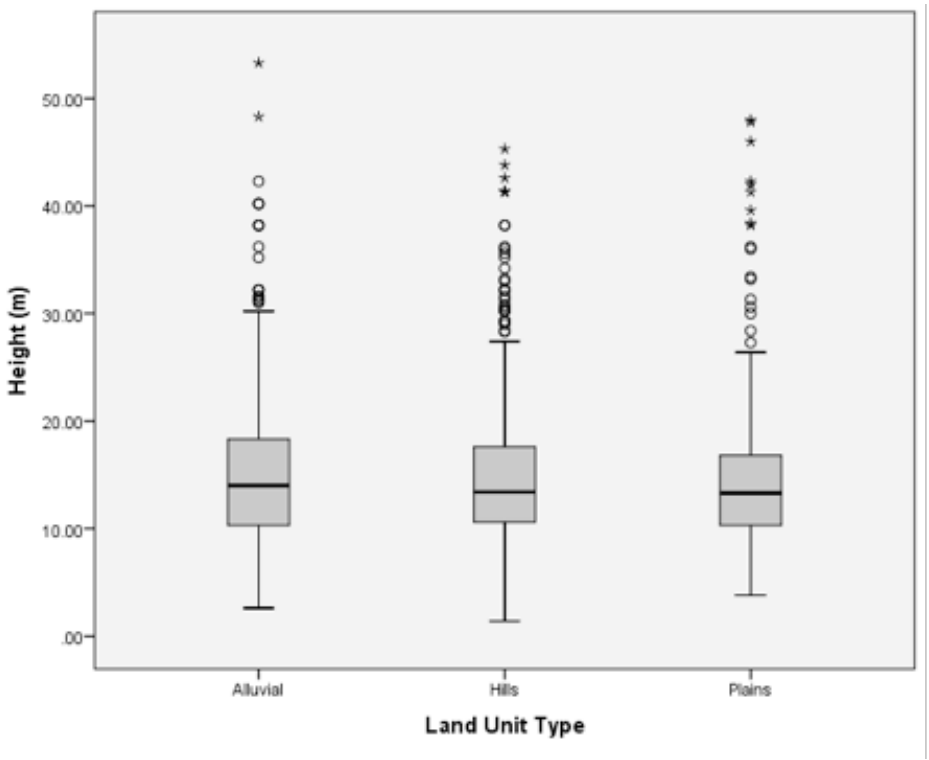

Figure 26. Pair-wise comparisons of tree heights between land units. Boxes represent quartiles, whiskers represent 95% quartile, * and ° refer to extremes and outliers, respectively. The extremes (*) can be considered emergent trees.

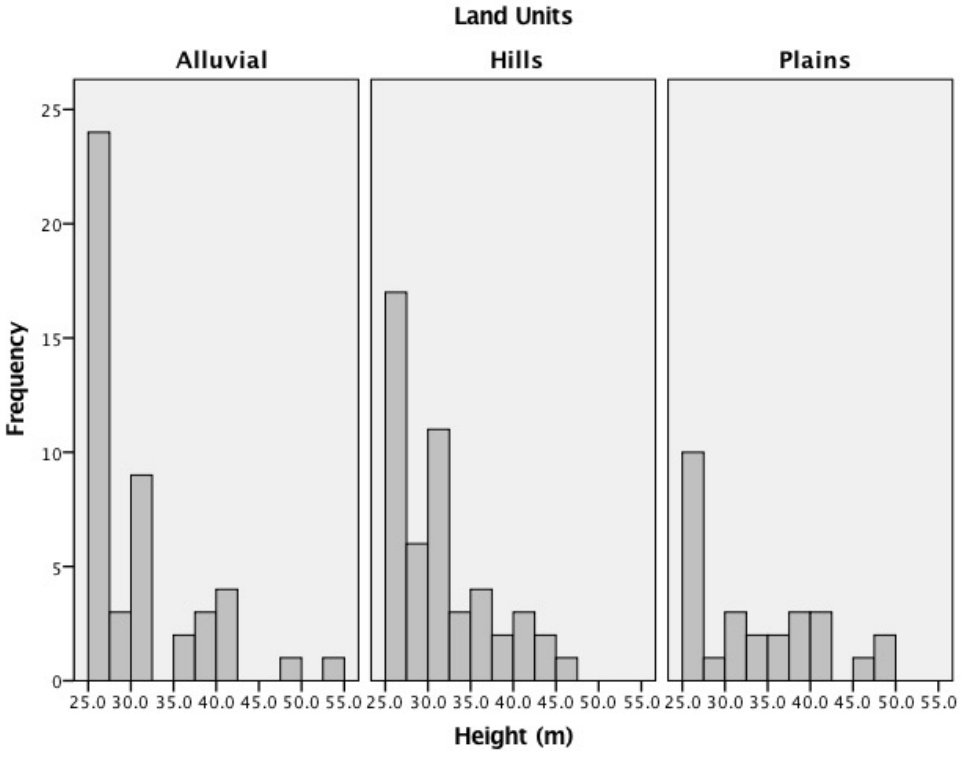

Figure 27. The frequency distribution of trees with heights >25m across the land units.

Table 5. A summary of the vegetation variables measured and calculated for each land unit.

	Alluvial			Plains			Hills			
	Q1	*Median*	*Q3*	*Q1*	*Median*	*Q3*	*Q1*	*Median*	*Q3*	*Kruskal-Wallis x^2 and P-value*
DBH (cm)	12.41	**17.82**	27.37	12.10	**15.92**	23.87	12.10	**15.60**	24.51	x^2=12.17; ***P* =0.002**
Bole Height (m)	6.0	**8.4**	12.3	6.2	**8.6**	11.6	6.6	**9.3**	12.4	x^2=7.29; ***P* =0.02**
Tree height (m)	10.3	**14.0**	18.3	10.3	**13.3**	16.9	10.6	**13.4**	17.6	x^2=3.99; *P* =0.14
Height/DBH ratios	57.12	**74.84**	92.77	59.31	**75.95**	96.47	63.65	**80.73**	98.41	x^2=13.12; ***P* =0.001**
Total number of trees ≥10cm†	22.0	**33.0**	47.0	32.0	**36.0**	41.0	23.5	**31**	35.5	x^2=1.81; *P*=0.40
Tree density (trees/ha) †	352.0	**528.0**	752.0	512.0	**576.0**	656.0	376.0	**496.0**	568.0	x^2=0.32; *P*=0.85
Stand basal area (m^2/ha) †	16.75	**27.20**	37.93	19.30	**25.61**	29.87	18.31	**24.28**	30.27	x^2=0.32; *P*=0.85

DBH= diameter at breast height
† Calculated from using plot data only

Table 6. A comparison of canopy branch availability for each size class across the three land units.

		Mean			Mann-Whitney *U*-test (*U*)					
Branches	Kruskal-Wallis (H)	Alluvial (*N*=569) (A)	Plains (*N*=549) (P)	Hills (*N*=579) (H)	**A vs. P**		**P vs. H**		**A vs. H**	
					U	*P*	*U*	*P*	*U*	*P*
<2cm	5.545^{ns}	2265.5±119.9	1808.3±101.1	2081.7±115.6	**151700**	**0.0166***	150800	0.1236^{ns}	151800	0.4060^{ns}
2-4 cm	10.08*	14.2±1.1	12.1±1.4	9.7±0.7	**147100**	**0.0005***	155000	0.4212^{ns}	**136100**	**0.00005***
4-10 cm	2.772^{ns}	5.4±0.4	4.5±0.6	4.1±0.6	**151000**	**0.0027***	151600	0.124^{ns}	**135000**	**0.000009***
10-20 cm	-13.17^{ns}	1.3±0.1	1.2±0.2	1.2±0.2	148300	0.0361^{ns}	153700	0.1273^{ns}	**151000**	**0.00027***
>20 cm	-22.39^{ns}	0.3±0.05	0.3±0.07	0.3±0.05	154600	0.4559^{ns}	158200	0.7378^{ns}	162300	0.2748^{ns}

Kruskal-Wallis: *Significant; ns=not significant
Mann-Whitney *U*-test: *Significant; ns=not significant (according to sequential Bonferroni probabilities corrections)

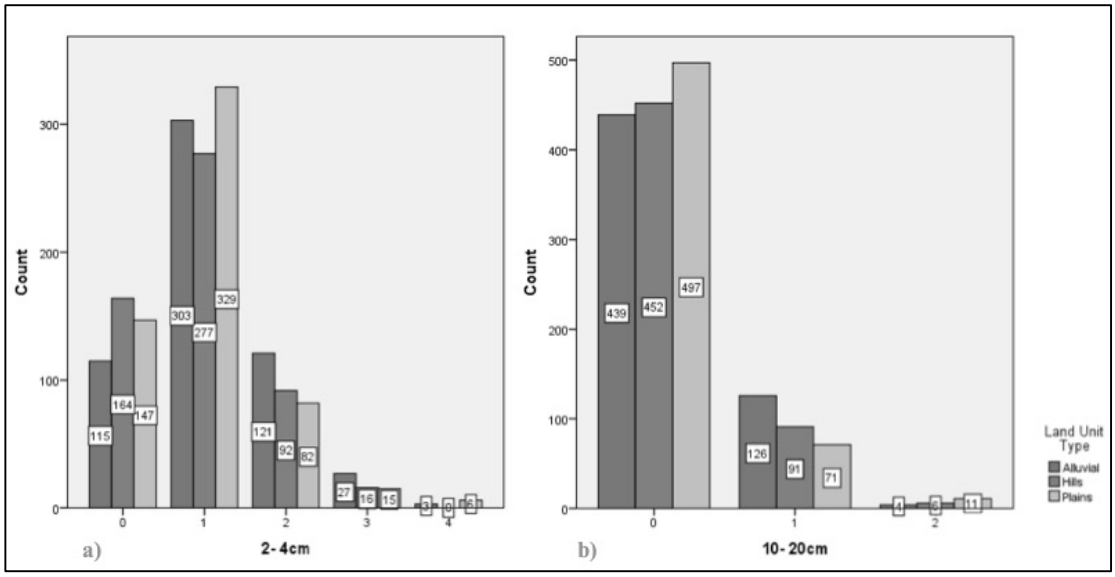

Figure 28. a) The frequency of 2-4 cm diameter supports; b) the frequency of 10-20 cm diameter supports available in each land unit. The numbers on the x-axis represent the number of branches recorded, represented as categories: 1 = 1-10; 2= 11-50; 3= 51-100; and 4= 101-500 branches.

4.2 Primate Group Density Estimates

4.2.1 Gibbon and siamang density estimates from density transects

Overall, 30 km of transects were sampled and no transect density data was collected on the primate species of interest since neither gibbons or siamangs were encountered along transects.

4.2.2 SECR Lar Gibbon Group Density Estimates

The number of groups detected was similar across sites but because the SECR model corrects for effective sampling area (which differed from 1.7 km^2 at the *Alluvial* site to 5.4 and 6.1 km^2 at the *Hills* and *Plains*) the estimated densities differed between land units. The *Alluvial* land unit had the highest density of gibbon groups at 2.85 groups/km^2, whereas the *Hills* and *Plains* had 0.86 and 0.44 groups/km^2 respectively (Table 7, Figure 29).

Detection function and detection surface estimates were used to build the SECR models and calculate effective sampling area (Figure 30, Appendix 1).

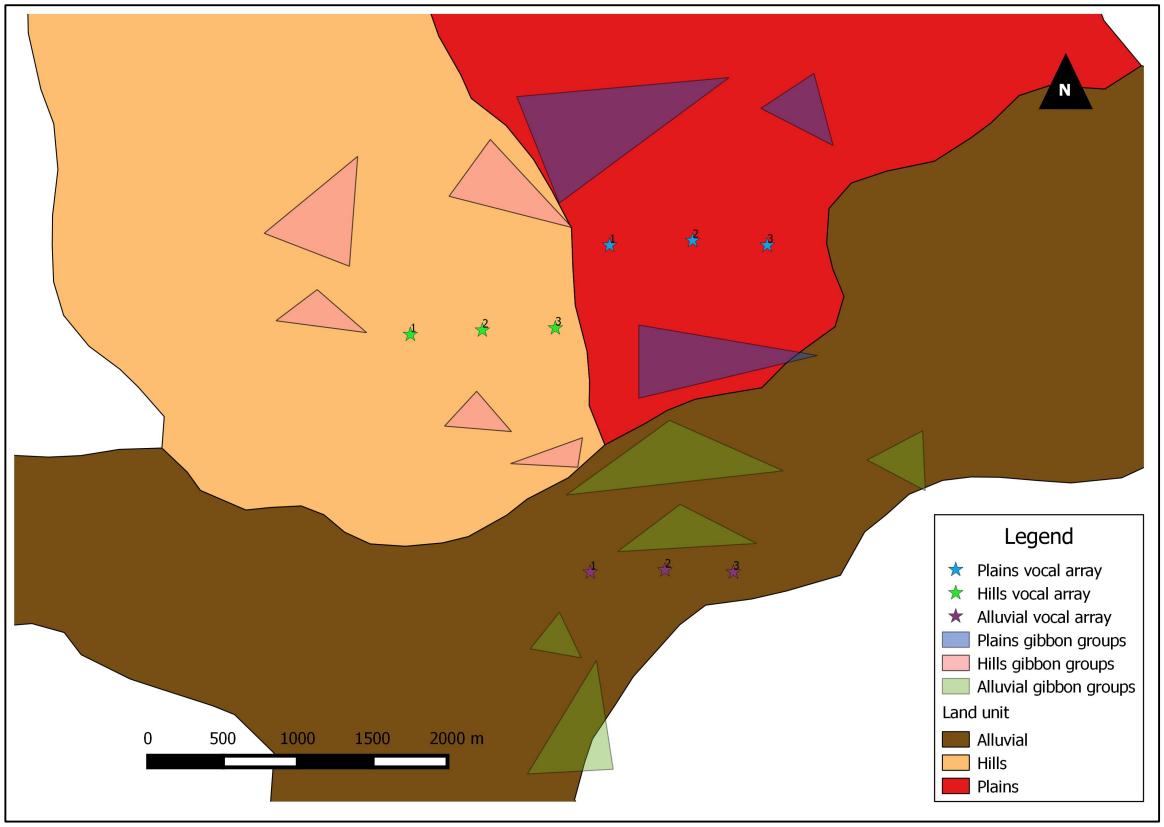

Figure 29. The number of gibbon groups identified at each land unit using triangulation methods. The placement of group polygons identifies approximate locations of gibbon groups heard during the four days using triangulation methods.

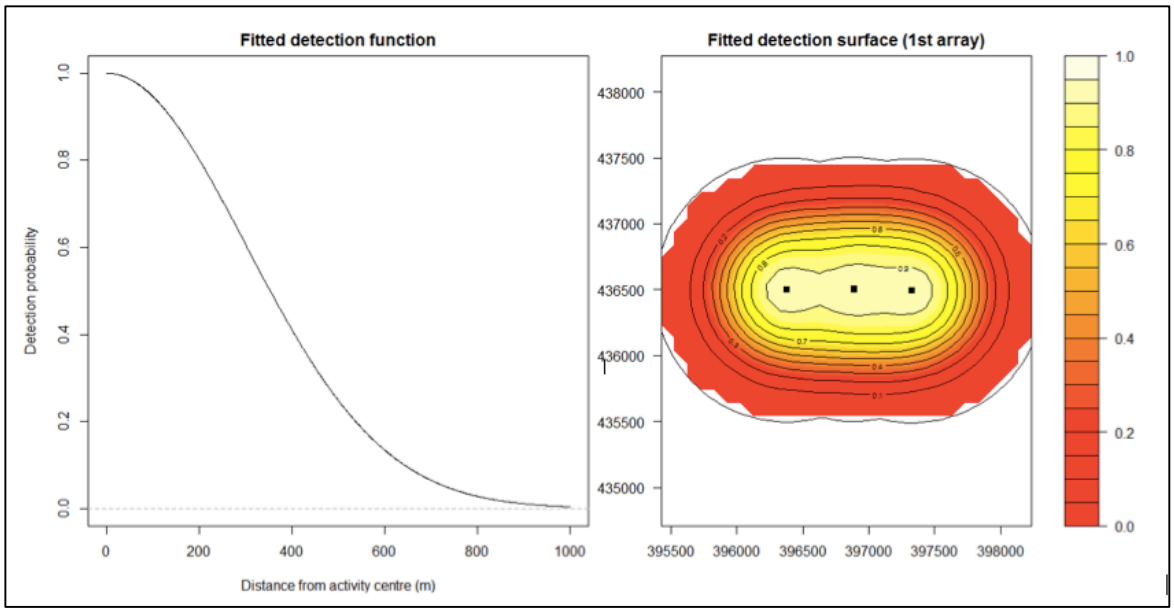

Figure 30. The detection function and detection surface for gibbons in the *Alluvial* land unit. Both figures illustrate that detection probability decreases as groups are located further from the listening posts (activity centres). If gibbons are located further than 1 km away from the listening posts, the probability of detecting their calls is close to 0.

4.2.3 SECR Siamang Group Density Estimates

The number of groups detected was similar across sites, but effective sampling areas differed from 3.3 km^2 at the *Alluvial* land unit to 4.2 and 6.1 km^2 at the *Hills* and *Plains*. Consequently, the estimated densities differed with the *Alluvial* land unit having the highest density at 1.52 groups/km^2, and *Hills* and *Plains* having 0.67 and 0.45 groups/km^2 respectively (Table 7, Figure 31).

Detection function and detection surface estimates showed a slightly greater effective detection for siamangs than gibbons (Figure 32, Appendix 1).

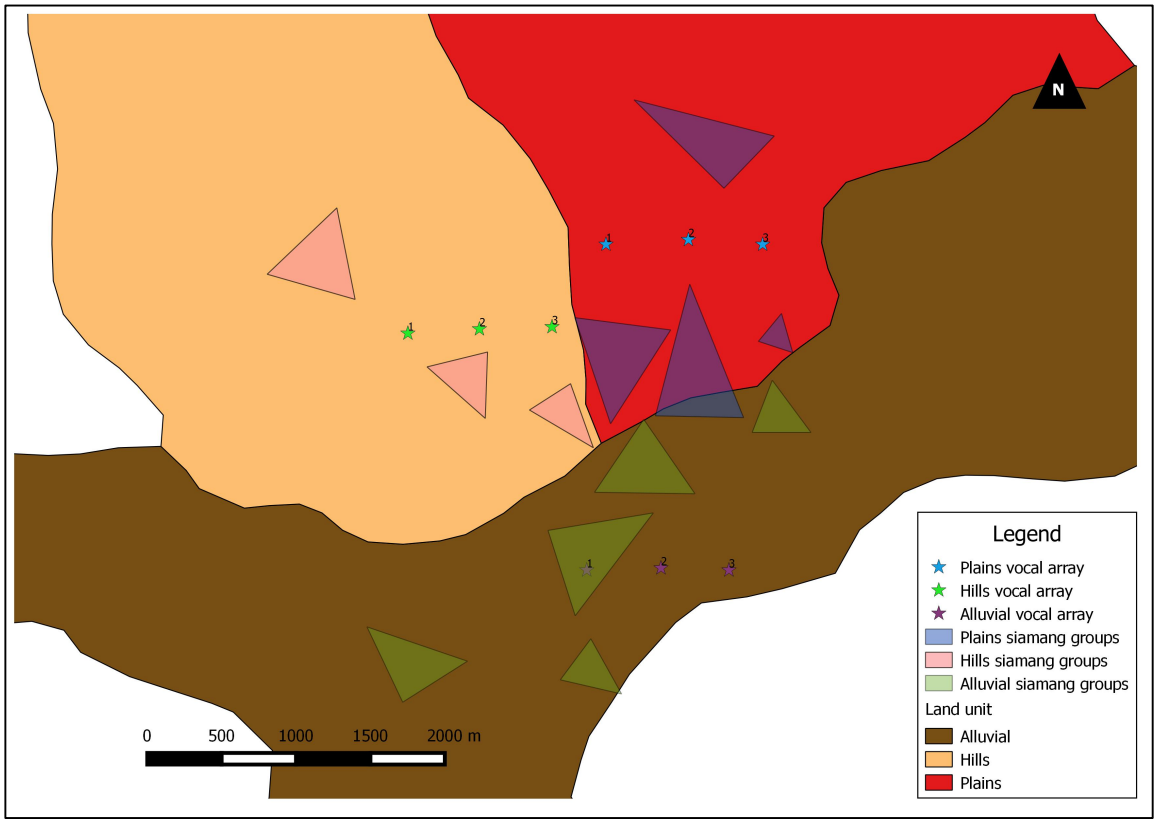

Figure 31. The number of siamang groups identified at each land unit using triangulation methods. The placement of group polygons identifies approximate locations of siamang groups heard during the four days using triangulation methods

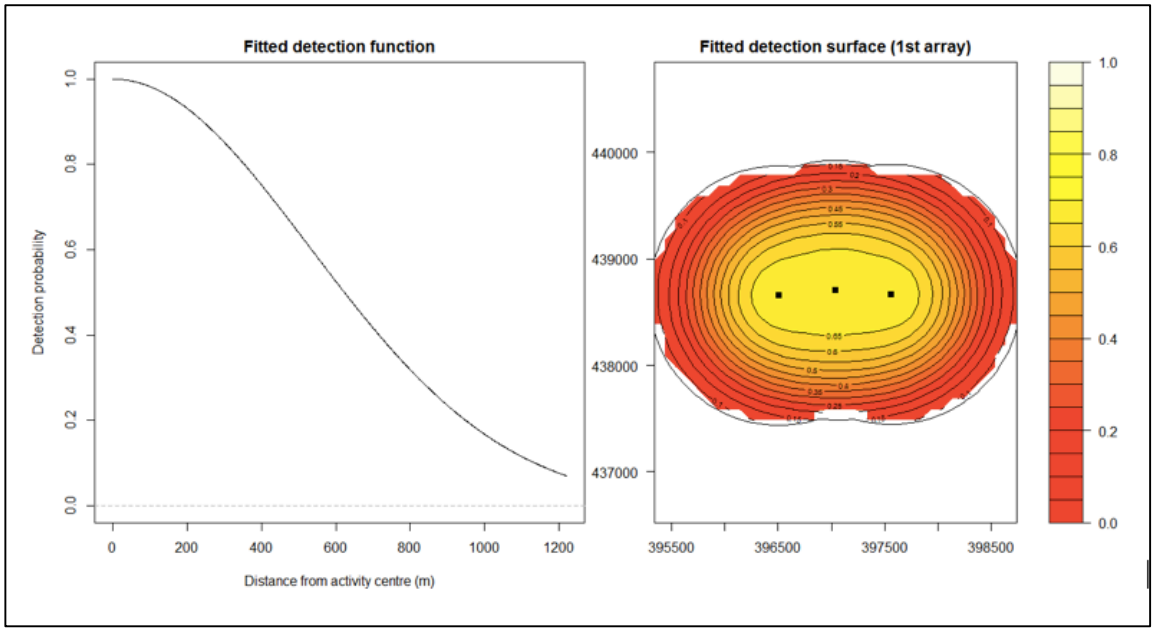

Figure 32. Example detection function and detection surface (siamangs in the *Hills*)

Table 7. Estimated Gibbon (*H.lar*) and Siamang (*S.syndactylus*) Group Densities and Calling Parameters from SECR models

Land Unit	Species	Group Heard (*N*)	Probability of calling *p*call	*E* (km^2)	Group density (groups/km^2)	Lower 95% C.I.	Upper 95% C.I.
Alluvial	*H.lar*	5	0.5	1.7	**2.85**	1.1	7.4
	S.syndactylus	5	0.35	3.3	**1.52**	0.65	3.8
Plains	*H.lar*	3	0.5	6.1	**0.44**	0.14	1.4
	S.syndactylus	4	0.5	6.1	**0.45**	0.14	1.4
Hills	*H.lar*	5	0.5	5.4	**0.86**	0.32	2.30
	S.syndactylus	3	0.25	4.2	**0.67**	0.19	2.29

E=effective sampling area; C.I.= Confidence Interval

4.3 Relationships between gibbon/siamang group densities and forest structure

The *Alluvial* land unit had highest group densities for both species and also had more large trees and more support branches than the other land units. However, there were no significant differences in the availability of the largest support size, >20cm, between the land units. The *Plains* had the lowest gibbon and siamang group densities and had significantly lower frequencies of trees >25m than the other land units.

5. DISCUSSION

The main aim of the study was to identify which forest structures are associated with the highest lar gibbon and siamang densities in a disturbed forest. The results of the vegetation and primate density group analyses showed that lar gibbon and siamang group densities were highest in the forest type classified as *Alluvial*, which also had the biggest (but not tallest) trees compared to the two other land units, *Hills* and *Plains*. This supports the hypotheses that there are differences between the land units within the Sikundur field site in both vegetation characteristics and primate densities, and these differences could be related to land unit characteristics and/or accessibility. It also supports the hypothesis that relatively more stratified forest types contain the highest primate densities.

5.1 Vegetation differences between land units

Tree height is an especially important indicator/ characteristic of habitat suitability for highly arboreal primates, such as gibbons and siamangs (Hamard et al. 2010). Gibbons and siamangs avoid travelling in lower canopies and show preferences towards travelling in high canopies (Cannon and Leighton 1994; Cheyne et al. 2013). The average tree heights across the three land units within this disturbed site were remarkably similar and are aggregated around heights of 13-14 m. Although median heights did not differ, the *Hills* and the *Alluvial* land units did have significantly greater frequencies of trees >25m than the *Plains*. Thus, differences in the frequency distributions of tall trees within each land unit may be an influential variable in determining Sikundur's primate group densities, but further investigation into this descriptive parameter is warranted. Furthermore, almost all of the heights recorded in Sikundur's forest were below 30 m and consequently this suggests that Sikundur's forest is not very tall in stature compared to other forests found in Gunung Leuser National Park (Laumonier 1997). Therefore, it is important not to extrapolate the results of this study to describe similar land units elsewhere.

Based on a review by Laumonier (1997) on Sumatra's forests, this study expected to find canopy heights of 25-30 meters with emergent trees reaching heights of 45 to 55 (or even 60) m. However, in this current study, no tree height was recorded above 55m. Out of 1704 vegetation samples, only 34 trees reached heights above 35 m (2%) and only six trees reached heights above 45 m (0.35%). These results illustrate that either 1) emergent trees are largely absent in this forest or 2) Sikundur's emergent trees exist with reduced heights. Although emergent trees were largely absent in Sikundur, a few emergent trees were encountered during data collection and were sampled in all three land units. The emergent trees of the *Alluvial* forest site reached greater heights than the emergent trees of the *Hills* and the *Plains*. These variations in tree heights amongst land units may be a consequence of

Sikundur's logging history and related to the accessibility differences amongst sites. It is likely that the tall emergent trees that were once present in the *Plains* and *Hills* may have been harvested to a greater extent by previous logging activities than the emergent trees found in the *Alluvial* forest. However, even though the heights of these emergent trees are reduced, their mere presence represents positive signs of forest regeneration, such that in the absence of severe logging pressures these trees have grown and matured into emergent trees. Overall, the presence of emergent trees in Sikundur's forest is very encouraging for the persistence of gibbons and siamangs as these trees will provide the layered and heterogenic canopy structure required for energy-efficient travel (Cannon and Leighton 1994).

Most of the regeneration or growth of trees that occurred post-logging are now clustered in the small (10-30 cm) and medium (31-60 cm) DBH size classes, rather than the large size classes (>60 cm) (Okuda et al. 2003). The *Alluvial* forest had a significantly higher frequency of medium sized trees than the other two land units. Possible explanations for these results could be related to different disturbance levels experienced by each land unit and accessibility differences. The *Alluvial* land unit was the only study site located across (south) the Besitang River, creating a physical separation between this forest type and the nearest local village. Therefore, in order for individuals to gain entry, they would have had to use a boat or cross the river by foot, which may have discouraged individuals from entering frequently. As a result, it is probable that the trees in the *Alluvial* forest experienced less frequent disturbances, which allowed them to grow to greater maturity levels and achieve larger stem diameters. On the other hand, the *Hills* and *Plains* were easily accessible by foot and even by motorbike. In fact, during the data collection period researchers encountered individuals on a more frequent basis in these study sites compared to the *Alluvial* site. Thus, the scarcity of medium sized trees in the *Plains* and *Hills* units may be a reflection of the higher disturbance levels experienced by these land units as a result of easy accessibility. A study by Southworth and Tucker (2001) in western Honduras recognized that forested areas in the most inaccessible locations, such as those located on steep slopes, at high elevations, and/or those furthest away from roads and towns, remained relatively undisturbed. Furthermore, this study also identified that most reforestation and regrowth only occurred at distances greater than 1 km away from roads and settlements. Accordingly, future research within the Sikundur region should aim to quantify accessibility differences between land units and examine if these differences correlate to the disturbance levels experienced by each forest unit. These variables may help explain structural differences of the forests observed between land units.

A study by Mugasha et al. (2013) reported that lowland forests tended to have a large diversity of *H:DBH* allometric relationships due to high tree diversity. As a result, there are likely a multitude of variables influencing the allometric relationships between a

tree's height and its diameter, such as its position in the the canopy, life-history characteristics or the abiotic characteristics of its habitat. Future research within Sikundur's forests could focus on determining the *H:DBH* allometric relationships of various tree species as these ratios can be used to develop accurate biomass estimates (Feldpausch et al. 2011) and be effective tools used to gauge deforestation rates (Mugasha et al. 2013). The *H:DBH* ratio of the *Hills* was significantly higher than the ratios for the other land units indicating that in the *Hills* the trees tended to consist of relatively faster growing species.

Although tree heights and canopy heterogeneity are important variables influencing gibbon and siamangs locomotion, this study was also interested in investigating the availabilities of different sized supports between land units. The *Alluvial* forest had the greatest range of different-sized supports available. Gibbons and siamangs show a significant preference for travelling in the main or upper canopy (Cannon and Leighton 1994; Cheyne et al. 2013). This may be a result of the fact that the main and upper canopies are likely to provide more stable and larger supports, which are more conducive to these primates' primary method of locomotion, which is brachiation.

Canopy connectivity is also implied as a major factor in the survival and fitness of arboreal primates as they have to rely heavily on connective canopies in order to gain access to food resources and to avoid predators (Anderson et al. 2007). In this study, there were no significant differences in canopy connectivity between the land units. This may be related to methodology or a real absence of differences. Thus, future studies looking to quantify differences in canopy connectivity between land units should also consider quantifying additional canopy variables, such as canopy cover, which is defined as as '*the proportion of the forest floor covered by the vertical projection of tree crowns*' (Korhonen et al. 2006, pp.578) or canopy closure, which is "*proportion of the sky hemisphere obscured by vegetation when viewed from a single point*" (Korhonen et al. 2006, pp.578). Hemispherical photos can be used as an efficient and simple method to calculate canopy cover and canopy closure and can be used to complement the crown connectivity measurements. These more in-depth analyses of forest canopies may reveal structural canopy differences between land units that were not apparent during this study.

The use of vegetation plots in addition to the line transects was beneficial because it allowed for a finer detection of vegetation differences between the land units (Hamard et al. 2010). Furthermore, the use of vegetation plots allowed specific vegetation parameters, such as tree density (trees/ha) or stand basal area (m^2/ha), to be calculated for each habitat site, which otherwise would not have been possible with the PCQM sampling methods alone. No significant differences in stand basal areas (m^2/ha) or tree densities (trees/ha) were detected between the three land units. A study conducted by Okuda et al. (2003) reported a stand basal area of 33.1m^2 ha^{-1} for a lowland dipterocarp primary forest and a stand basal area of

34.0 $m^2 ha^{-1}$ for a regenerating forest. However, this study calculated stand basal areas of 24 - 27 $m^2 ha^{-1}$, slightly lower than Okuda et al.'s (2003) sites. Similarly, a study by Hall et al. (2003) in central Africa compared the SBA between an unlogged forest and a logged forest site. The unlogged forest stand had a higher basal area of 30.5 $m^2 ha^{-1}$, whereas the logged stand 18-years post logging had a basal area of 24.4 $m^2 ha^{-1}$ (Hall et al. 2003). Hall et al. (2003) also found that the basal area of the logged site was 19% lower than that of the unlogged site. The basal areas of the logged forests in the study by Hall et al. (2003) resemble the basal areas obtained from this current study for all land units, which further illustrate the regenerating nature of Sikundur's forest. Sikundur's forest is likely still in the process of regeneration and it will take many more decades for this forest to resemble its pre-logging conditions.

5.2 Group Densities

The results of this study indicate that the *Alluvial* site had the highest group densities for gibbons and siamangs than the other two land units, with group density estimates of 2.85 groups/km^2 and 1.52 groups/km^2 respectively. On the other hand, the *Plains* had the lowest group densities for both lar gibbons and siamangs, 0.44 groups/km^2 and 0.45 groups/km^2 respectively. As for the *Hills*, group densities for both lar gibbons and siamangs were intermediate at 0.86 for gibbons and 0.67 groups/km^2 for siamangs. The density estimates obtained from this study should be treated with caution due to the use of a reduced buffer, which limited the effective sampling area. Consequently, groups heard within the focal land up but located outside of this buffer were removed from the analyses. This could have influenced the derived density estimates.

The group density estimates for gibbons in the *Alluvial* land unit are comparable to other published density estimates, however the siamang group density estimate of *Alluvial* and the density estimates for gibbons and siamangs in the other land units are much lower than previous estimates (Table 8). These differences could be related to 1) specific properties of the site and land units or 2) methodological differences. First, the site's previous logging history and other anthropogenic disturbance activities may help explain why Sikundur has low group density estimates. The *Plains* and *Hills* land units were located north of the Besitang River and were easily accessible as a basic path/road leading to the Sikundur field camp existed. Furthermore, Sikundur has an existing trail system with some trails beginning right off the road/path. Access into the *Hills*, which was once difficult, has become incredibly easy as the trail system penetrates far into the Sikundur forest and even extends into the southeastern portion of the *Hills* land unit. Unfortunately, during data collection,

local villagers were encountered on numerous occasions in these forest sites. These disturbances, either big or small, can greatly influence the ecology and behaviour of gibbons and siamangs and lead to underestimates of group densities. Johns (1985) observed that gibbons' calling rates were instantly reduced following the initiation of logging activities mid-way through their study's data collection. Consequently, the group density estimates obtained from this study for gibbons and siamangs in these two land units may in fact be an underestimation of their true group densities due to the likelihood of local disturbances negatively influencing these primates' behaviours and ecologies. Future research in Sikundur should sample the primate densities of the primary forest located within Sikundur's vicinity (~10 km). Sampling the primate densities of this primary forest could provide a comparative basis into how Sikundur's disturbance history has influenced the resident primates and associated densities. Furthermore, future comparisons between the primary forest and Sikundur in primate densities and also forest structure could help quantify and evaluate the types of disturbances impacting the Sikundur field site.

Secondly, this study differs methodologically from previous studies by using a new developed SECR density estimation model compared to the more traditional Brockelman and Ali (1987) method. Brockelman and Ali (1987) calculate primate group densities using the formula $D = n/E$, where E is the effective listening area (Buckley et al. 2006). A common difficulty in this approach is determining the effective sampling area (ESA), which has been described as the sampling area where at least two of the three listening posts can hear vocalizing primate groups up to 1 km away (Buckley et al. 2006). Consequently, ESA estimates have been prone to error (Kidney et al. 2013). On the other hand, using SECR models for primate surveys has many advantages over the traditional method because these models provide a more realistic estimate of ESA by incorporating spatial information from listening posts and they can estimate overall group densities (Kidney et al. 2013). If a primate's average calling probability is calculated for a sample period, i.e. 4 days, SECR models can estimate overall group densities, not just the densities of calling groups (Kidney et al. 2013). Furthermore, SECR models also account for imperfect detections by incorporating detection functions and using species calling probabilities.

Within the primatology field, the application of SECR models to determine primate group density estimates is relatively new and different than previous methods used to determine group density estimate. Consequently, these systematic differences in determining density estimates may be responsible for the observed variation between this study's group density estimates and previously published estimates, as illustrated by Table 8. Furthermore, the gibbonsSECR package in R (developed by Darren Kidney, University of St Andrews; available at: //github.com/dkidney/gibbonsSECR) used to run the SECR models is still in the process of being developed and therefore this program still demonstrates performance

limitations. It would be beneficial for future models to be able to incorporate shape files, such as those of a study site. These modifications may provide more accurate estimates of the effective sampling area, which in turn will provide more precise group density estimates.

Table 8. Group Density Estimates of Gibbons and Siamangs obtained from this study and past studies.

Species	Group Density (groups/km^2)	Site	Reference
Lar Gibbon (*Hylobates lar*)	2.85[1]	Sikundur, North Sumatra	This study
	0.44[2]	Sikundur, North Sumatra	This study
	0.86[3]	Sikundur, North Sumatra	This study
	5	Khao Yai National Park, Thailand	Brockelman et al. (1998)
	2.6	Phu Khieo Wildlife Sanctuary, Thailand	Borries et al. (2002)
Agile Gibbon (*Hylobates agilis*)	1.0	Way Canguk Research Station, Sumatra	O'Brien et al. (2004)
	1.7	Sabangau catchment, Kalimantan	Hamard et al. (2010)
	2.0[5]	Kerinci-Seblat National Park, Sumatra	Yanuar (2009)
	3.8[6]	Kerinci-Seblat National Park, Sumatra	Yanuar (2009)
Bornean Agile Gibbon (*Hylobates agilis albibarbis*)	2.16	Sabangau catchment, Kalimantan	Buckley et al. (2006)
Siamang (*Symphalangus syndactylus)*	1.52[1]	Sikundur, North Sumatra	This study
	0.45[2]	Sikundur, North Sumatra	This study
	0.67[3]	Sikundur, North Sumatra	This study
	3.6	Way Canguk Research Station, Sumatra	O'Brien et al. (2004)
	5.4[4]	Kerinci-Seblat National Park, Sumatra	Yanuar (2009)
	5.0[5]	Kerinci-Seblat National Park, Sumatra	Yanuar (2009)
	2.1[6]	Kerinci-Seblat National Park, Sumatra	Yanuar (2009)
	3.2[7]	Kerinci-Seblat National Park, Sumatra	Yanuar (2009)

[1]Group density estimate from *Alluvial* land unit; [2]Group density estimate from *Plains* land unit; [3]Group density estimate from *Hills* land unit; [4]montane forest; [5]lowland forest.[6]hill dipterocarp; [7]submontane

Brockelman and Ali (1987) summarized data from 5 populations of lar gibbons and suggested that the probability of calling (p) should be above 0.5 (Brockelman et al. 1998). However, the calling probabilities obtained during this study were always ≤0.5 for lar gibbons and siamangs in all land units. A mix of factors may be responsible for these low values. Firstly, this study was only able to obtain small sample sizes due to limited manpower in the field and a restricted time frame for sample collection. Furthermore, vocal sampling for the primate groups in this study were only conducted during a single season. A study by Brockelman and Srikosamatara (1993) demonstrated that gibbon calling is influenced greatly by weather conditions and seasonal variation. The results of their study demonstrated that gibbons sang more frequently during the summer season opposed to the cool monsoon season (Brockelman and Srikosamatara 1993). Thus, it would be wise to expand the data collection of this study to include several more sampling periods that can be distributed across the different seasons. Secondly, as stated by Johns (1985) 'the absence of singing does not mean that gibbons are absent from the area'. Past research has shown that a

group's calling frequency was influenced by the area's overall group densities. For example, groups with fewer neighbours may become less vocal and sing less than gibbons found in areas with higher group densities (Brockelman and Srikosamatara 1993). Therefore, auditory sampling methods may have underestimated group densities in study sites that have low densities.

In addition to auditory sampling, primate density line transects were completed in order to provide supplementary data to the auditory data collection. However, these density transects were unsuccessful in providing supplementary data. Out of 60 transects, primates were only observed on three occasions and on all occasions the primate species observed were long-tailed macaques. This study found that the significant problem related to the density walks was that primates in the distance fled immediately or became immobile in the high canopies, making detection near impossible. As a consequence, these behaviours prevented proper species identification and further data collection. Johns (1985) reported a 25% decrease in the number of primate groups encountered once logging was initiated at the field site. Johns (1985) linked this decrease in primate encounters to the primates' behavioural changes, such as an increase in freezing behaviours or a decrease in conspicuous activities such as feeding or travelling (Nijman 2001).

The results of this study should provide a basis for future studies interested in investigating primate group densities for the Sikundur region. Although this study was unable to provide adequate sample sizes for detecting significant group density differences between land units, these results can be used for future comparisons and it has helped to outline efficient sampling methods specific to this field site. Furthermore, the group densities observed for both gibbons and siamangs in the *Alluvial* site are comparable to previous published estimates, which helps reiterate the fact that degraded habitat sites can support viable primate populations and consequently make significant contributions to conservation efforts (Lee et al. 2014). The next step for lar gibbon and siamang research in the Sikundur region would be habituation. Primate habituation would allow future researchers to determine group sizes through visual observations and provide accurate population estimates by determining the number of individuals per km^2. Furthermore, Cheyne et al. (2008) also advise that visual observations such as those from density transects can be used to provide supplementary data to auditory sampling and subsequently help researchers obtain more accurate population estimates. These population estimates will be vital in implementing and prioritizing future conservation strategies.

5.3 Primate group densities and related vegetation characteristics

The *Alluvial* land unit displayed the highest primate group densities for both primate species and it was also the land unit with higher frequencies of medium-sized trees and taller (>25m)

trees. Past studies have correlated high primate densities to tree height (Umpathy and Kumar 2000; Hamard et al. 2010), which may also be the case for this forest type, but further research is needed. The *Alluvial* land unit also had the highest availabilities of different-sized supports overall. The presence of larger-sized supports is likely an important structural feature of gibbons and siamangs' habitats as these primates tend to brachiate along larger sized supports (Fleagle 1980), thus the varied range of supports available within the *Alluvial* forest may have positively influenced its hylobatid group densities. Furthermore, a study by Manduell et al. (2012) reported that orang-utans (also partly brachiating) at a field site in Ketambe, which displayed a large variation in the types of supports available, were able to make use of various locomotor/support combinations as a result of their heterogeneous arboreal environment (Manduell et al. 2012). Furthermore, the availabilities of specific support types and sizes that were conducive to orang-utan locomotion likely facilitated energetically advantageous locomotor behaviours (Manduell et al. 2012). These same concepts can be assumed to be applicable to gibbons and siamangs and their specialized form of locomotion for the *Alluvial* land unit. Consequently, the *Alluvial* forest displays vegetative and structural characteristics that are favourable in supporting greater primate group densities and this supports the hypothesis that the forest type with the most stratified and structurally complex canopy will have the highest primate group densities.

On the other hand, the *Plains* land unit had the lowest group densities for both species, which is likely related to it being highly exploited by local villagers as a result of its easy accessibility. The *Plains* vegetation displayed a low frequency of both large (DBH) and tall trees >25 m, which consequently suggests that the canopy is less stratified and structurally complex. Thus, the structural characteristics of the *Plains'* vegetation supports the first hypothesis that forest structure between the land units will be different as a result of accessibility. Consequently, the habitat suitability of the *Plains* may not meet the requirements of highly arboreal primates, such as gibbons and siamangs, and as a result very low primate densities were recorded in this land unit.

Additional habitat-related factors, such as food abundance or parasite load, have been shown to influence primate densities. For example, a study by Marshall and Leighton (2006) examined whether fruit abundance limited the Bornean white-bearded gibbon (*Hylobates albibarbis*) population densities in Gunung Palung National Park in West Kalimantan, Indonesia. The results indicated that total food availability was uncorrelated with gibbon density, therefore suggesting that these gibbon populations were not limited by food abundance (Marshall and Leighton 2006). However, the results did show that Bornean gibbon densities were highly correlated with the abundance of figs, an important fall-back

food for gibbons (Marshall and Leighton 2006). This example helps illustrate that although this current study examined whether forest structure and vegetation could help explain observed primate group densities, other important habitat-related variables such as the abundance of fall-back foods or the degree of human disturbances could also be influencing Sikundur's gibbon and siamang densities and should be examined in future primate studies within Sikundur.

6. IMPLICATIONS FOR CONSERVATION

Indonesia's tropical lowland forests are ranked third in the world in terms of their biological richness (Harris et al. 2008). In addition, these forests provide important ecosystem services such as fresh water management and pollination services and also act as the largest storage systems of natural carbon (Kettle 2010). Unfortunately, few undisturbed primary forests remain in the tropics, whereas the numbers of degraded or secondary forest types are continually increasing (Gibson et al. 2011). Up to 60% of the world's remaining tropical forests are categorized as degraded or secondary forests and as a consequence the conservation efforts only dedicated to protecting primary or old-growth forests may no longer be rational or beneficial (Dent and Wright 2009). Accordingly, recent studies have highlighted the importance of restoring and protecting previously degraded habitats and secondary forests as they have been demonstrated to be valuable in maintaining biological diversity.

As of recently, conservation studies have evaluated the differences in species diversity and richness between primary and degraded/logged forests. Surprisingly, the results indicated that logged forest types displayed compatibility in supporting and maintaining substantial levels of biodiversity. For example, a study by Berry et al. (2010), which compared differences in species diversity between primary and logged sites, found that even though the logged forest had lower faunal species richness, these differences were normally not greater than 10%. Furthermore, 90% of the species recorded in the primary forest were also present in logged forests, including species of conservation concern (Berry et al. 2010). Consequently, future conservation strategies should concentrate on the restoration and regeneration of degraded forest types including those that have been previously logged (Dent and Wright 2009; Berry et al. 2010; Kettle 2010; Gibson et al 2011). A top priority for policy makers should be the prevention of logged forests from being converted to oil palm and other agricultural crops since the latter result in the most severe losses in biodiversity (Wilcove et al. 2013). Oil palm plantations and the construction of associated road networks required for transportation purposes represent the most serious of threats regarding the deforestation of lowland forests (Gaveau et al. 2009). REDD initiatives would likely be effective conservation strategies and highly applicable in regions where palm-oil expansions are occurring. Identifying the optimal areas where REDD interventions could be implemented should be a conservation priority as this would help reduce deforestation rates, as well as generate revenue (Harris et al. 2008). Furthermore, the benefits accumulated from REDD interventions would not only be represented by the amount of land saved from deforestation, but also be evident in the population estimates of forest-dwelling vertebrates, such as primates. Previously affected primate species would benefit by REDD's increased

protection efforts because they would be given more time to either adapt to local conditions and/or successfully increase their population numbers.

7. CONCLUSIONS AND RECOMMENDATIONS

The main results obtained from this study are:

- The *Alluvial* land unit had the highest gibbon group densities, 2.85 groups/km^2, and the highest siamang group densities, 0.44 groups/km$^{2.}$
- The *Plains* land unit had the lowest gibbon group densities, 0.29 groups/km^2 and the lowest siamang group densities, 0.45 groups/ km^2.
- The *Alluvial* forest differed significantly with one of the other two sites, or both, for the following variables: DBH; bole height; number of branches for 0-2cm, 2-4cm, 4-10cm, 10-20cm diameter size classes; *H:DBH* ratio; frequency of trees >25m; frequency of medium-sized trees (31-60cm).
- The *Plains* had a significantly lower frequency of medium sized trees ($31 \leq DBH \leq 60$) and a significantly lower frequency of trees taller than 25m.
- No significant differences between land units were found for the following variables: % canopy connectivity; crown shape; tree density (trees/ha); and stand basal area (m^2/ha).

The main recommendations drawn from this study are:

- To incorporate the use of visual observations of primates to boost the accuracy of vocal group density estimates.
- To expand the vocal data collection of this study to include several more sampling periods and to distribute them across the different seasons
- Primate habituation is the next step for primate research in Sikundur.
- Canopy connectivity is an important structural feature for many arboreal primates, such as gibbons and siamangs. Accordingly, a combination of methods should be used to quantify canopies at various forest sites and the use of hemispherical photos is an easy and efficient sampling method.
- The evaluation of disturbance and accessibility levels amongst land units in Sikundur is needed in order to understand their impacts on forest structure, and consequently primate group densities.
- Provide continued protection to degraded and logged-over habitat sites within the Sikundur region as they are compatible with primate conservation
- Identify if Sikundur's forests and communities would benefit from REDD interventions as palm-oil expansions may occur within this region in the near future

Conclusion:

A forest's suitability in supporting primate populations may be partially dependent upon the structural characteristics of its vegetation. This study focused on quantifying the differences in primate densities and vegetation characteristics between three disturbed land units in Sikundur, North Sumatra. This study's results supported both hypotheses related to vegetation and accessibility differences, as well as primate differences between land units. The *Alluvial* site was the least accessible and consequently this land unit had larger trees (DBH), higher frequencies of tall trees >25m, and a greater availability of various branch sizes than the other two land units (*Plains* and *Hills*). The *Alluvial* forest was also the land unit with the highest group densities for both primate species. On the other hand, the *Plains* was the most accessible and displayed a lower frequency of larger (DBH) and tall trees >25m. Consequently, these vegetation characteristics may be related to why the *Plains* had the lowest primate group densities for both species. The results of this study can be used to help illustrate the important conservation value degraded and logged forests have in supporting primate populations and help provide more protection towards these forest types.

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9. APPENDIX I

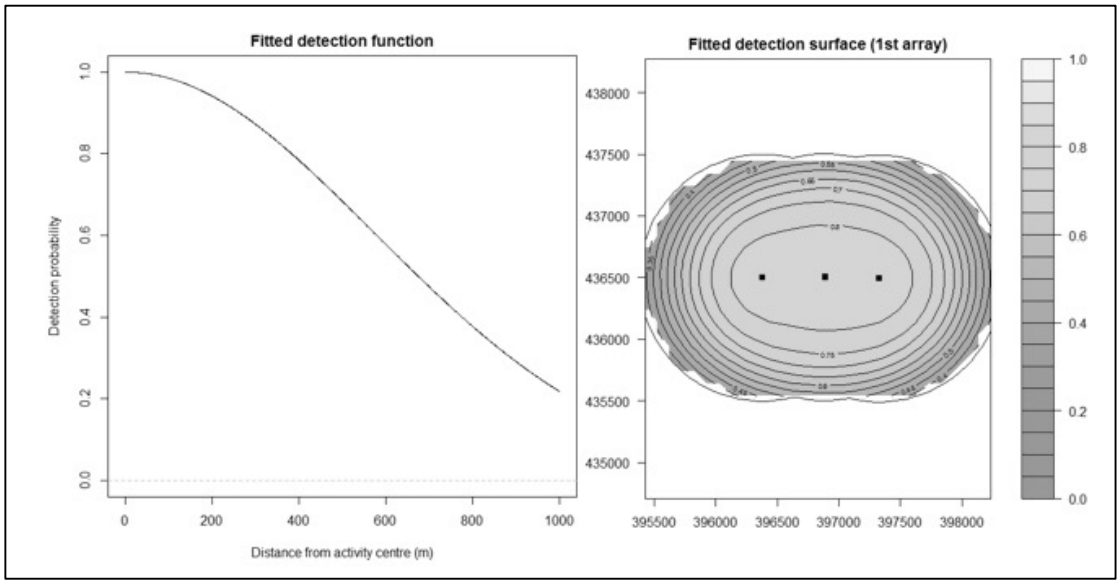

Figure 1. Detection function and detection surface for siamangs in the *Alluvial* forest type.

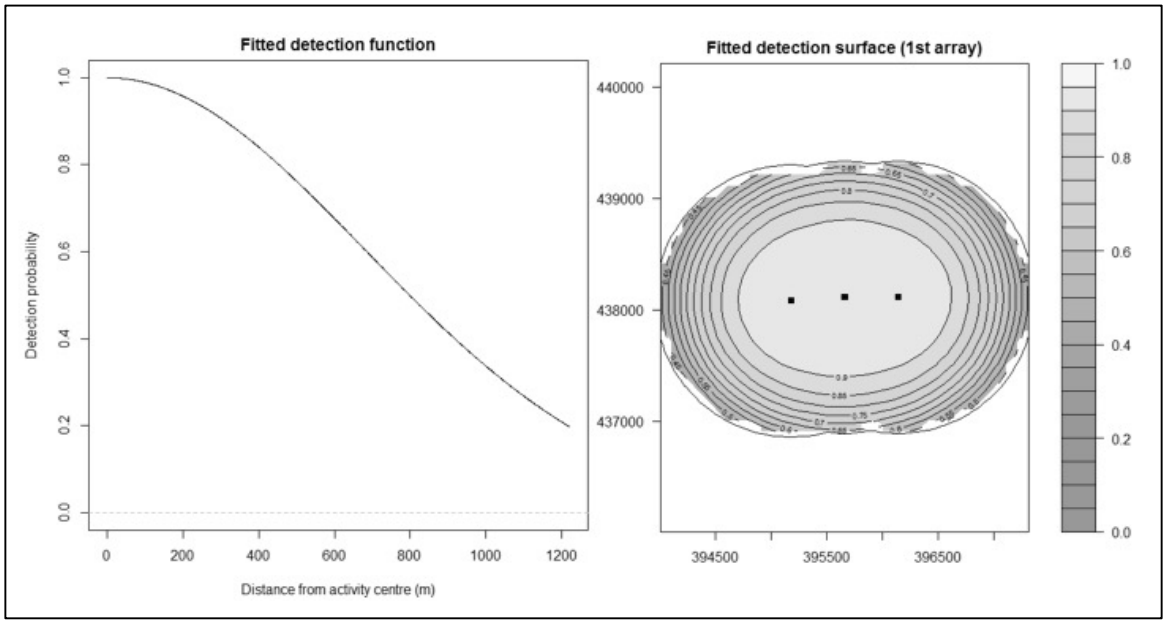

Figure 2. Detection function and detection surface for gibbons in the *Hills* forest type

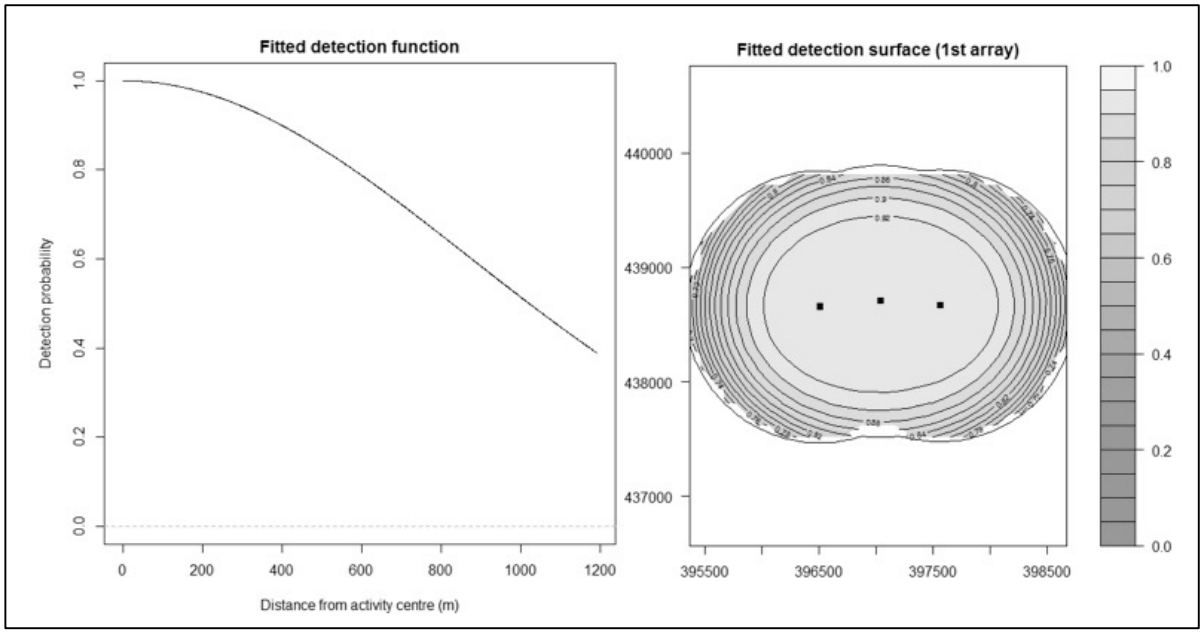

Figure 3. Detection function and detection surface for gibbons in the *Plains* forest type

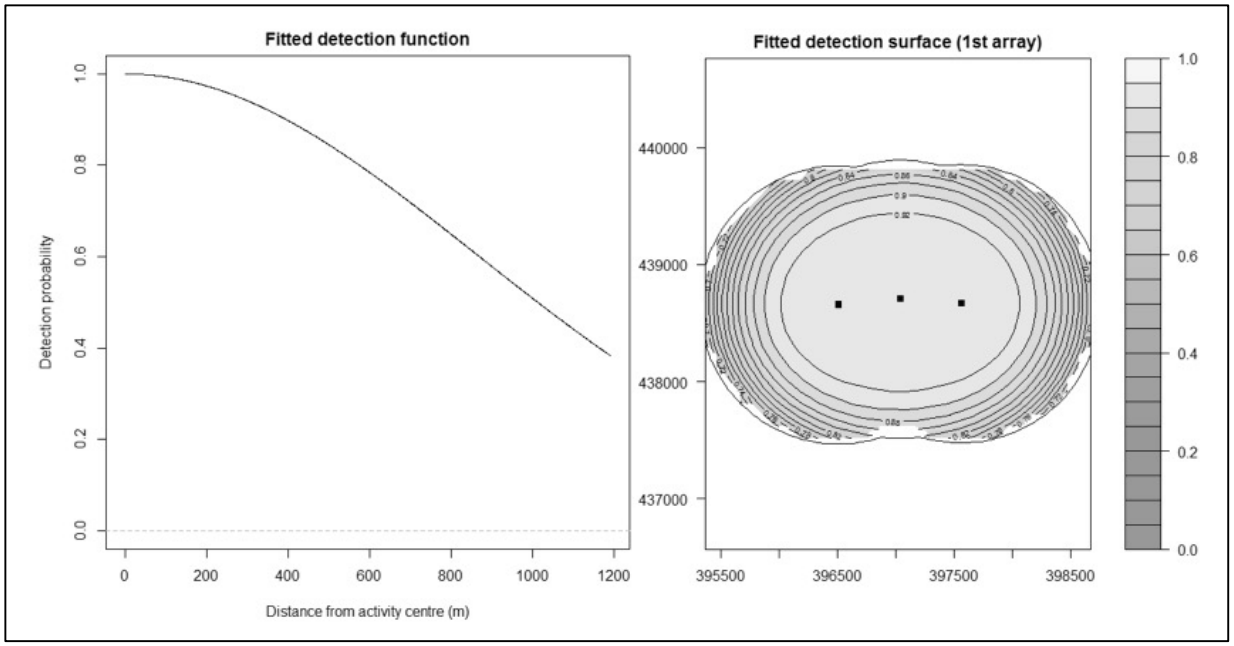

Figure 4. Detection function and detection surface for siamangs in the *Plains* forest type